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BATS OF THE WEST INDIAN ISLAND OF DOMINICA: NATURAL HISTORY, AREOGRAPHY, AND TROPHIC STRUCTURE

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INTRODUCTION

Because the islands in the Caribbean long have interested students of mammals and zoogeography, considerable information has been published concerning the biology of the Antillean mammalian fauna in the past three decades (Jones and Schwartz, 1967; Schwartz and Jones, 1967; Koopman, 1968, 1989; Jones and Phillips, 1970, 1976; Varona, 1974; Baker and Genoways, 1978; Baker et al., 1978; Swanepoel and Genoways, 1978; Jones and Baker, 1979; Silva Taboada, 1979; Baker et al., 1984; Eshelman and Morgan, 1985; Buden, 1986; Griffiths and Klingener, 1988; Jones, 1989; Masson et al., 1990; Pederson et al., 1996; Genoways et al., 1998). This increasing interest in the systematics and zoogeography of mammals in the region has involved both studies in the field and re-examination of collections made in earlier years. One problem facing investigators who attempt to assess the faunal relationships of the Antilles is the fact that natural conditions on most islands have been altered significantly as a result of early settlement, first by Ameridians, then by Europeans beginning in the 1500s. Changes wrought by agricultural practices have destroyed much of the original environment, and introduction on many islands of the mongoose (*Herpestes javanicus*) as a supposed means of controlling introduced rats (both *Rattus norvegicus* and *R. rattus*) has disturbed natural conditions.

One island favorable for the investigation of the natural history of mammals is Dominica, the northernmost of the Windward Islands. With an area of 800 square kilometers, Dominica is the third largest island in the Lesser Antilles (only Guadeloupe and Martinique are larger). The island is approximately 45 kilometers long and 24 kilometers wide at the widest point. It is located near the center of the Lesser Antillean chain, between 15°10' and 15°40' north latitude, and 61°15' and 61°29' west longitude; Guadeloupe to the north and Martinique to the south are about equidistant (approximately 40 kilometers) from the island. The smaller Marie Galante is only 30 kilometers to the northeast. Dominica contains the highest and most rugged terrain of any in the Lesser Antilles, and is one of the few islands where mongoose have not been introduced. Beard (1949:108) noted that Dominica is 80 percent forested, and it remains the most pristine of any in the Lesser Antilles. The forest is mainly rain forest although much is secondary owing to shifting

agricultural practices. Land under cultivation generally is scattered along the coasts, especially in small pockets on the alluvial plains of the many rivers, whereas the center of the island is mostly forested.

The dominant physiographic feature of the island is a north-south mountain chain. The highest point is Morne Diablotin (1450 m) in the north-central part of the island; Morne Trois Pitons (1400 m) is the tallest peak in the south-central part of the island. These peaks are surpassed in height in the Lesser Antilles only by Morne Soufriere on nearby Guadeloupe. A plateau, lying between two chains of mountains at an altitude of 460 m to 610 m, covers the center of the island. There are at least eight mountains around this plateau with an elevation of 915 m or more and two smaller peaks higher than 610 m.

The Layou River, the largest river on the island, flows westward between Morne Diablotin and Morne Trois Pitons and drains in the central plateau. Most of the rivers on Dominica flow east or west from the precipitous heights of the center of the island. Deep ravines and youthful valleys radiate from all the mountains and are bordered by ridges that generally run to the coast, ending in sea-cliffs, especially on the north and south ends of the island. Because of the rugged nature of the interior and the lack of extensive flatlands along the coasts, the vegetation has been disturbed less by agriculture than on most, if not all, other islands of the Lesser Antilles.

The climate of the Lesser Antilles varies considerably over a short distance (Beard, 1949). The general climate pattern on Dominica is a dry season from January through May and a hurricane season from July to September. Major hurricanes occur approximately every 15 to 20 years, with the most recent being Hurricane David in 1979 and to a lesser extent Hurricane Hugo in 1989. A "dry belt" climate is present on the leeward coast (Beard, 1949), where rainfall measures between 900 mm to 1670 mm a year; mean annual temperature is about 26°C and the mean relative humidity is approximately 75 percent. The remainder of the island consists of "mountain and upper mountain belt" climate (Beard, 1949). More than 2565 mm of rainfall is regularly recorded at windward coast weather stations, more than 5130 mm at the stations

in the zone of rain forest, and precipitation may be as much as 10,250 mm on the highest mountain peaks, although exact measures on peaks are unrecorded (Hodge, 1954). Relative humidity seldom falls below 85 percent in the interior of the mountain and upper mountain belt. Temperature averages about 21°C, but temperature varies with altitude and season with the lowest temperatures in February and March.

The first published reference to a bat collected on Dominica was by Oldfield Thomas (1891) in reference to *Ardops nicholli*. H. S. Branch in 1901 made significant collections of bats on the island and A. H. Verrill made a small collection of bats there in 1906. Few specimens were collected in the half-century that followed; however, in the late 1950s through the mid-1970s, in addition to herpetological investigations, Albert Schwartz and associates obtained bats on Dominica and other Antillean islands on several occasions. J. Knox Jones, Jr., under the aegis of the Bredin-

Archbold-Smithsonian Biological Survey of Dominica, visited the island on three occasions, beginning in 1966 when he collected from late March until late April. He returned to the island in 1967 accompanied by Carleton J. Phillips when they collected from August 27 until September 2. Finally, Jones visited Dominica with Robert J. Baker from July 19 to 27, 1978. Other specimens of bats from Dominica in the collections of the Museum of Texas Tech University were obtained when Robert D. Owen and classes of students collected in June and July of 1991 and 1992. These investigations resulted in the collection of large series of bats, thereby providing the materials for an up-to-date survey of the chiropteran fauna of Dominica. These specimens were accompanied by a wealth of natural history information, which is summarized here. With completion of this major survey, we have taken the opportunity to investigate the areography (Udvardy, 1969) of this island's chiropteran fauna to gain a better understanding of its position within the West Indies.

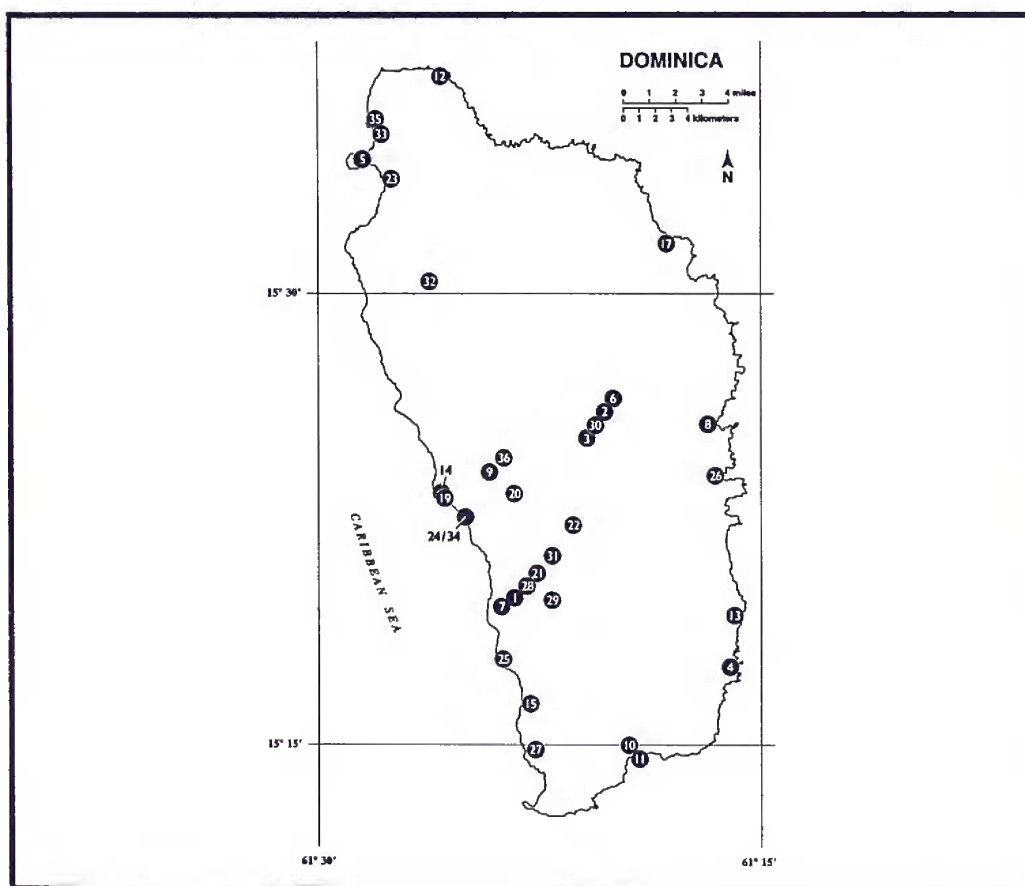


Figure 1. Reference points for localities of specimens of the chiropteran fauna of Dominica. Numbers correspond with locations listed in gazetteer.

METHODS

All measurements in the accounts that follow are in millimeters and weights are given in grams. Forearms and crania were measured with dial or digital calipers. External measurements other than forearm are those recorded on specimen labels by collectors. Measurements of the maxillary toothrow are of the greatest alveolar length; greatest length of skull includes incisors; forearms were measured from the posterior extension of the radius-ulna to the most anterior extension of the carpels; length of ear was measured from notch to tip. All measurements of embryos are

of crown-rump length. Capitalized color terms are from Ridgway (1912).

Specimens listed as examined are in the collection of the University of Kansas Natural History Museum (KU), the National Museum of Natural History (NMNH), Museum of Comparative Zoology, Harvard University (MCZ), Texas Cooperative Wildlife Collection, Texas A&M University (TCWC), and Museum of Texas Tech University (TTU).

GAZETTEER

Numbers indicate localities as presented in Figure 1.

1. Antrim Valley		St. Paul Parish	15°20'N, 61°23'W
Basin Well	[=Basin Will]		
Bassinville	[=Basin Will]		
2. Bassin Will		St. Joseph Parish	15°26'N, 61°20'W
3. Bells		St. Joseph Parish	15°25'N, 61°21'W
Belvédère	[Belvidere]		
4. Belvidere		St. Patrick Parish	15°17'N, 61°15'W
5. Cabrit		St. John Parish	15°35'N, 61°29'W
6. California Estate		St. Joseph Parish	15°26'N, 61°20'W
7. Canefield		St. Paul Parish	15°20'N, 61°24'W
8. Castle Bruce		St. David Parish	15°26'N, 61°16'W
9. Clarke Hall Estate		St. Joseph Parish	15°24'N, 61°25'W
10. Geneva		St. Patrick Parish	15°15'N, 61°19'W
11. Grand Bay		St. Patrick Parish	15°14'N, 61°19'W
12. Là Haut		St. Andrew Parish	15°38'N, 61°26'W
13. La Plaine		St. Patrick Parish	15°20'N, 61°15'W
14. Layou		St. Joseph Parish	15°24'N, 61°26'W
15. Loubier	[=Loubiere]	St. George Parish	15°17'N, 61°23'W
16. Mahaut		St. Paul Parish	15°22'N, 61°24'W
17. Marigot		St. Andrew Parish	15°32'N, 61°18'W
18. Massacre		St. Paul Parish	15°21'N, 61°24'W
Mourne de Moulrier		St. George Parish	[approx. east of Roseau, not located]
19. mouth Layou River		St. Joseph Parish	15°24'N, 61°26'W
20. Mt. Joy		St. Paul Parish	15°24'N, 61°24'W
21. Mt. Joy Estate		St. Paul Parish	15°21'N, 61°22'W
22. Ponte Cassé		St. Paul Parish	15°22'N, 61°21'W
23. Portsmouth		St. John Parish	15°35'N, 61°28'W
24. Rodney's Rock		St. Paul Parish	15°23'N, 61°25'W
25. Roseau		St. George Parish	15°18'N, 61°24'W
26. Saint Sauveur		St. David Parish	15°24'N, 61°16'W
27. South Chiltern Estate		St. Luke Parish	15°15'N, 61°22'W
28. Springfield		St. Paul Parish	15°21'N, 61°22'W
29. Stinking Hole Cave	[above Cochrane]	St. Paul Parish	15°20'N, 61°22'W
Stone Estate	[=Stone Hill Estate?]		
30. Stone Hill Estate		St. Joseph Parish	15°26'N, 61°21'W
31. Sylvania		St. Paul Parish	15°22'N, 61°22'W
32. Syndicate		St. Peter Parish	15°31'N, 61°26'W
33. Tanetane		St. John Parish	15°36'N, 61°28'W
34. Tarou Point		St. Paul Parish	15°23'N, 61°25'W
35. Toucari		St. John Parish	15°37'N, 61°28'W
West Cabrit	[=Cabrit]		
36. York Valley Estate		St. Joseph Parish	15°25'N, 61°24'W

SYSTEMATIC ACCOUNTS

Family MORMOOPIDAE

Pteronotus davyi davyi Gray

Davy's Naked-backed Bat

Specimens examined (58).—ST. GEORGE PARISH: Roseau, ca. 50 ft, 2 (NMNH 113189-90). ST. JOHN PARISH: Tanetane, 5 m, 21 (TTU 31306-26). ST. JOSEPH PARISH: 1 mi. above mouth of Layou River, 5 m, 1 (TTU 31327). ST. LUKE PARISH: South Chiltern Estate, ca. 1300 ft, 2 (NMNH 361895, 360296). ST. PATRICK PARISH: Grand Bay, sea level, 8 (NMNH 361894, 391218-24); Belvédère Estate, ca. 500 ft, 1 (NMNH 113570). ST. PAUL PARISH: Antrim Valley, 2 (TTU 31305, 31328). PARISH UNKNOWN: "Dominica," 21 (MCZ 7012; NMNH 113572-90, 113592).

Additional records.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985). PARISH UNKNOWN: Dominica (Smith, 1972:100).

Remarks.—Davy's naked-backed bat is known in the Lesser Antilles from Marie Galante (off Guadeloupe), Dominica, Martinique, and Grenada. Although the species has not been reported from islands between Martinique and Grenada, it is reasonable to assume that it will be found elsewhere in the Windward chain, and possibly on some of the other Leeward Islands. *Pteronotus davyi* and *P. parnellii*, recently reported from St. Vincent (Vaughan and Hill, 1996), are the only mormoopid bats known to occur in the Lesser Antilles. These species can be easily distinguished by the larger size of *P. parnellii* and that the wing membranes of *P. davyi* fuse along the mid-dorsal line, whereas the wing membranes of *P. parnellii* attach lower on the sides so that the mid-dorsal area is covered by a band of hair.

Smith (1972) revised species of the family Mormoopidae and recorded *P. d. davyi* as occurring in Nicaragua, Costa Rica, Venezuela, Trinidad, and on several Lesser Antillean islands. Although noting some

Table 1.—Measurements of *Pteronotus davyi davyi* from Dominica and Trinidad.

Measurement	Dominica				Trinidad			
	Mean	(range)	N	SE	Mean	(range)	N	SE
Length of forearm	46.6	(45.4-48.3)	8	±0.30	46.8	(45.2-48.3)	5	±0.65
Greatest length of skull**	16.2	(16.0-16.5)	8	±0.07	15.9	(15.8-16.1)	5	±0.07
Condylbasal length	15.0	(14.8-15.3)	8	±0.07	14.8	(14.7-14.9)	5	±0.04
Zygomatic breadth	9.2	(8.8-9.3)	8	±0.04	9.3	(9.2-9.4)	5	±0.04
Postorbital constriction*	3.7	(3.5-3.9)	8	±0.03	3.8	(3.6-3.8)	5	±0.04
Breadth of braincase*	8.3	(8.0-8.5)	8	±0.04	8.1	(7.9-8.3)	4	±0.09
Mastoid breadth	9.0	(8.8-9.2)	8	±0.04	8.9	(8.7-9.2)	5	±0.13
Rostral breadth	7.1	(7.0-7.4)	8	±0.04	7.1	(6.9-7.4)	5	±0.09
Breadth across upper molars	6.2	(6.0-6.3)	8	±0.02	6.3	(6.2-6.4)	5	±0.04
Length of maxillary toothrow	6.8	(6.7-6.9)	8	±0.03	6.8	(6.6-6.9)	5	±0.06

*= $P \leq 0.05$

**= $P \leq 0.01$

variation within populations of *P. d. davyi*, Smith concluded that all were best assigned to the nominate subspecies. We concur, noting that specimens from Dominica differ significantly from individuals from Trinidad (type locality of *davyi*) in three cranial dimensions (Table 1, greatest length of skull, postorbital constriction, and breadth of braincase) and in having a somewhat higher braincase, a better-developed sagittal crest, and more pronounced indentation on the dorsal surface of the rostrum. Smith (1972:100) noted that *davyi* undoubtedly invaded the Lesser Antilles from northern South America or Trinidad and wrote: "I suspect this invasion is relatively recent (perhaps Late Pleistocene), judging from the absence of any noteworthy morphological differences between Dominican specimens and those from northeastern South America."

Smith (1972:48-49) found little secondary sexual variation in any species of mormoopids, including samples of *P. davyi*. Measurements of adults from Dominica, which are listed in Table 2, tend to confirm this result. In the one external and eight cranial measurements given, the only character revealing significant secondary sexual variation was breadth of braincase. In this measurement, males averaged significantly larger than females at the $P \leq 0.05$. For the remaining measurements, males and females averaged the same in two (breadth across upper molars and length of maxillary toothrow), males averaged larger in three (greatest length of skull, condylobasal length, and zygomatic breadth), and females averaged larger in three (length of forearm, postorbital constriction, and mastoid breadth).

Specimens of *P. davyi* from Dominica have been obtained in January, March, June, July, and October. The known altitudinal range is from sea level to approximately 400 m. Two specimens were taken on March 25, 1964, in a mist net set among trees in the yard of the estate house at South Chiltern. Eight were captured by knocking them from the air with sticks as they flew around a light that had been stationed to attract insects at Grand Bay on March 13, 1964; the collectors suspected that the bats were attracted by "swishing" sounds made by movement of sticks through the air. Two naked-backed bats were taken in a mist net set over the water works tank at Antrim Valley on July 20, 1978, and another was captured in a

net set under mango trees that separated cacao groves at a place along the Layou River about 1 mile from the mouth on the evening of July 21, 1978. The largest sample of this species was taken from a small cave above Douglas Bay near Tanetane. The mouth of the cave was about 5 m wide and 2.5 m high, but inside the space quickly narrowed to smaller passages. Baker, who entered the cave, estimated the population at several thousand *Pteronotus*.

Three adult females from Grand Bay were all in early stages of pregnancy and each was carrying a single embryo when captured on March 13. Embryos averaged 6.3 (5 to 7) in crown-rump length. The weight of six March-taken males averaged 9.3 (8.8 to 9.8); three pregnant females weighed 9.2, 9.3, and 9.8. Three females taken on July 21, 22, and 27 were not pregnant; however, a second female taken on July 27 was lactating. Seven males taken on July 27 had testes that averaged 4.0 (2.5 to 5.0) in length.

Family NOCTILIONIDAE

Noctilio leporinus mastivus (Dahl) Big Fishing Bat

Specimens examined (9).—ST. GEORGE PARISH: Roseau, 1 (TCWC 55804); ST. JOSEPH PARISH: mouth of Layou River, sea level, 6 (KU 104762-64, NMNH 361893, 391216-17); 1 mi. above mouth of Layou River, 5 m, 1 (TTU 31294); Clarke Hall Estate, 100 ft, 1 (KU 104761).

Additional record.—PARISH UNKNOWN: "Dominica" (Jones, 1951).

Remarks.—This large fish-eating bat is widely distributed in the American tropics and is on record from many of the Lesser Antillean islands (see Jones and Phillips, 1970:137; Baker and Genoways, 1978; Jones, 1989; Koopman, 1989). Howes (1930:101) first mentioned the occurrence of the "fish bat" on Dominica, but indicated that his party obtained none. The first actual specimens from the island were reported by Jones (1951:224). Hall and Kelson (1959:87-88) referred Lesser Antillean bats to the subspecies *Noctilio leporinus leporinus* (type locality restricted to Suriname by Thomas, 1911:131), but noted that "sub-

Table 2.—Length of forearm and cranial measurements of representatives of three chiropteran families (Mormoopidae, Noctilionidae, and Natalidae) from Dominica.

Sex and statistics or catalog number	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Mastoid breadth	Breadth across upper molars	Length of maxillary tooththrow
<i>Pteronotus davayi davayi</i> (males)									
N	5	5	5	5	5	5	5	5	5
Mean	46.5	16.3	15.1	9.2	3.6	8.4	9.0	6.2	6.8
Minimum	45.4	16.1	14.8	9.1	3.5	8.3	8.8	6.1	6.7
Maximum	46.9	16.5	15.3	9.3	3.7	8.5	9.1	6.3	6.9
±SE	±0.28	±0.09	±0.09	±0.05	±0.04	±0.04	±0.05	±0.03	±0.04
<i>Pteronotus davayi davayi</i> (females)									
N	3	3	3	3	3	3	3	3	3
Mean	46.8	16.1	14.9	9.1	3.7	8.2	9.1	6.2	6.8
Minimum	45.9	16.1	14.8	9.0	3.6	8.2	9.0	6.2	6.7
Maximum	48.3	16.2	15.0	9.3	3.7	8.3	9.2	6.2	6.8
±SE	±0.76	±0.03	±0.06	±0.09	±0.03	±0.03	±0.07	±0.00	±0.03
<i>Noctilio leporinus mastivus</i> (male)									
NMNH 361893	88.8	27.6	25.0	20.0	7.1	13.9	18.5	12.8	—
<i>Noctilio leporinus mastivus</i> (females)									
N	4	4	4	4	4	4	4	4	1
Mean	88.1	26.2	24.0	19.3	7.0	13.8	17.1	12.6	10.3
Minimum	86.3	25.9	23.8	19.1	6.7	13.4	16.8	12.5	
Maximum	89.6	26.6	24.1	19.5	7.3	14.0	17.5	12.7	
±SE	±0.68	±0.16	±0.07	±0.09	±0.12	±0.13	±0.15	±0.05	
<i>Natalus stramineus stramineus</i> (males)									
N	9	9	9	9	9	9	9	9	9
Mean	39.6	16.9	15.4	8.6	3.2	8.1	7.5	5.6	7.2
Minimum	37.1	16.2	14.5	8.1	3.0	8.0	7.2	5.2	7.0
Maximum	41.0	17.3	15.8	8.9	3.3	8.2	7.8	5.8	7.6
±SE	±0.42	±0.13	±0.13	±0.08	±0.03	±0.02	±0.08	±0.07	±0.08
<i>Natalus stramineus stramineus</i> (females)									
N	7	6	6	7	7	7	7	7	7
Mean	38.8	16.7	15.4	8.5	3.2	7.8	7.4	5.5	7.1
Minimum	38.2	16.5	15.1	8.4	3.1	7.6	7.2	5.2	7.0
Maximum	39.6	17.1	15.5	8.7	3.3	8.1	7.5	5.7	7.1
±SE	±0.18	±0.11	±0.06	±0.04	±0.03	±0.07	±0.04	±0.08	±0.02

specific allocation of specimens from the northern [islands]...is uncertain." Husson (1962), however, pointed out the small size of typical *leporinus* from Suriname, and Koopman (1968:2) was inclined to refer all Lesser Antillean populations and bats from Trinidad to the larger subspecies *mastivus*. Davis (1973) reviewed geographic variation in *N. leporinus* and referred all Antillean specimens to *N. l. mastivus*, a subspecies to which he ascribed a distribution including not only the entire Antillean region but also Middle America and northern South America.

External and cranial measurements of an adult male and four adult females from Dominica are given in Table 2. Although no significance testing for secondary sexual variation could be done, it should be noted that measurements of the male were outside the range of measurements of the females in five characters (greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, breadth across upper molars). These results are similar to those found by Davis (1973) for populations of this species in Chiapas.

Principally, *Noctilio leporinus* probably occurs in coastal areas where bays and estuaries provide quiet water for fishing, and within a few miles of the coast along at least some of the larger rivers. Most of the numerous rivers and streams on the island are too small or fast flowing, or both, to provide adequate feeding grounds for fishing bats. Six of our nine specimens are from the mouth of the Layou River on the Caribbean side of the island. Another was taken in nets set under mango trees that separated cacao groves near the Layou River about a mile from its mouth. None was taken in a large mist net set across the Layou River at this point, although several fishing bats were observed avoiding the net. The eighth was taken in a mist net stretched over a trail through forest adjacent to the Layou River approximately two miles upstream from the coast at Clarke Hall. The mouth of the Layou is broad, and opens into a small bay where sandy barriers form a broad brackish water estuary between the river and the Caribbean. The last mile or so of the Layou itself is relatively broad and quiet, quite in contrast to the upper reaches, and the river and adjacent bay at this site provide an ideal foraging area for fishing bats. Several of our specimens were obtained over an area of the estuary. Few other kinds of bats were

seen at this place. Finally, the specimen from Roseau is the partial skeleton of an old individual of unknown sex recovered from the floor of a small cave near the main highway north of the city where it intersects with the road to the Hummingbird Inn.

A female netted on March 23, two shot on April 24, and another taken on April 25 all were pregnant with a single fetus. Crown-rump lengths of fetuses of the first three females listed were 16, 32, and 41, respectively. A female taken on July 22 was lactating. The adult male weighed 68.1; two of the pregnant females weighed 63.4 and 64.1. Dominican specimens examined for ectoparasites carried only a tick, *Ornithodoros hasei* (Schulze), a species also recorded on fishing bats in Trinidad, Brazil, and Panama.

A male taken on April 2 and females obtained on March 23 and July 22 are brownish to orange-brown dorsally and orange to ochraceous-buff ventrally; the remainder of our specimens (taken from early February to late April) have dull brownish dorsal coloration and are much paler ventrally. The difference may be related to annual molt in this genus, but we found no physical evidence of molt on any of the specimens examined (see also Davis, 1973:864).

Family PHYLLOSTOMIDAE

Brachyphylla cavernarum cavernarum Gray Antillean Fruit-eating Bat

Specimens examined (56).—ST. DAVID PARISH: 2 3/4 mi. W Saint Sauveur, 400 ft, 1 (KU 104803). ST. JOSEPH PARISH: Clarke Hall Estate, 100 ft, 14 (KU 104792-802, 110148-50). ST. LUKE PARISH: South Chiltern, ca. 1300 ft, 2 (NMNH 361898-99). ST. PAUL PARISH: 6 mi. NE Roseau, 1100 ft, 3 (KU 150743-45); Springfield, 1 (TTU 31447); Stinking Hole Cave, above Cochrane, 22 (TTU 31425-46). PARISH UNKNOWN: "Dominica," 13 (NMNH 113615-27).

Additional record.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985).

Remarks.—The genus *Brachyphylla* is endemic to the Antilles, where two species are currently recognized (Swanepoel and Genoways, 1978). *Brachyphylla*

nana, which occurs on Cuba, Grand Cayman, Middle Caicos, and Hispaniola, is much smaller than *B. cavernarum* (Swanepoel and Genoways, 1978). Indeed, there is no overlap in range of measurements when the sexes of the two species are compared separately for condylobasal length and zygomatic breadth. Swanepoel and Genoways (1983) present a key to these species. Swanepoel and Genoways (1978) previously found enough secondary sexual dimorphism in *Brachyphylla cavernarum*, with males being generally larger than females, to warrant treating them separately in morphology analyses. However, in measurements of our sample from Dominica (Table 3), we found no significant secondary sexual variation. The sexes averaged the same in three characters (postorbital constriction, breadth across upper molars, and length of maxillary toothrow). The average for the sexes was within 0.2 mm for all other characters, with males being larger in all except length of forearm. Additionally, there is individual variation in color, varying from a medium brown (such as Prout's Brown) to as dark as Mummy Brown.

Brachyphylla cavernarum cavernarum is known to occur on St. Croix in the Virgin Islands and throughout the Lesser Antillean islands as far south as St. Vincent, excepting Barbados. The species is represented by separate subspecies on Puerto Rico and the remaining Virgin Islands (*intermedia*) and on Barbados (*minor*). This bat is widespread in the Antilles and seems to be fairly common on Dominica.

The genus *Brachyphylla* is here placed in the subfamily Phyllostominae and the Tribe Glossophagini (Baker et al., 1989), rather than in the monotypic subfamily Brachyphyllinae (Koopman, 1993; Wetterer et al., 2000).

All bats of this genus collected on Dominica in 1966 and 1967—total of 15—were taken with mist nets. On March 23, 1966, a single individual was captured in a net strung in a banana grove at Clarke Hall Estate. In late March and early April, five *Brachyphylla* were taken in a net set across a gravel bar in the Layou River and adjacent to vegetation lining the river; other kinds of bats taken at this place with *Brachyphylla* were *Ardops*, *Artibeus*, *Monophyllus*, and *Sturnira*. In late April a net at this same site again captured *Brachyphylla*, *Ardops*, and *Artibeus*. Two nets set on

April 19 and 21 in a banana-coconut grove adjacent to the Layou River at Clarke Hall Estate yielded *Brachyphylla*, *Artibeus*, and *Monophyllus* (this grove yielded three *Brachyphylla* and many *Artibeus* between August 29 and September 2, 1967). A net set in a banana grove by the Fond Figue River, 2 3/4 mi. W Saint Sauveur, St. David Parish, took only a single *Brachyphylla* on April 20. A net set at Clarke Hall Estate, across a trail bordered by a banana grove and vegetable plot with widely spaced trees, yielded *Brachyphylla*, *Artibeus*, and *Sturnira* in April of 1966. The only Antillean fruit-eating bats taken by Jones and Baker in July 1978 came from Stinking Hole Cave near Cochrane. The hole was about 20 m deep with sharply inclining passages leading in two directions. A small sulphur-smelling stream emerged from the hole. Baker entered the hole and reported seeing several thousand *Brachyphylla*, including young. Some of the young appeared virtually hairless and pinkish in color so they were probably neonates.

Usual weather conditions may not affect the activity of this bat, although the few individuals netted during this study do not allow definite interpretation. Specimens of this bat have been collected on Dominica during the months of February through September.

Reproductive data were collected during the spring of 1966, mid-summer 1978, and late summer of 1967. All females collected in 1966 contained a single embryo—one on April 8 carried an embryo measuring 33 and two taken on April 19 had embryos measuring 35 and 41. A female captured on September 2, 1967, was lactating as were four of ten females, checked for reproductive activity, captured in the maternity colony in Stinking Hole Cave on July 26, 1978. Five males collected between March 23 and April 8 had testes that averaged 5.6 in length (5 to 6). Four males collected from April 19 through April 23 had testes that measured slightly smaller than the earlier-taken males, averaging 4.9 (4 to 5.5). Three males removed from Stinking Hole Cave on July 26 had testes that measured 2.5, 4, 4 and two males taken on August 30 and September 2, 1967, had testes that were 7 and 6, respectively. A juvenile female was collected on July 16, 1901, by H. S. Branch. This specimen has epiphyseal phalanges that were incompletely fused, but the forearm measurement, 63.6, is within the range of adults.

Table 3.—Length of forearm and cranial measurements of five species of the chiropteran family Phyllostomidae from Dominica.

Sex and statistics	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Mastoid breadth	Breadth across upper molars	Length of maxillary tooththrow
<i>Brachyphylla cavernarum cavernarum</i> (males)									
N	5	5	5	5	5	5	5	5	5
Mean	63.9	31.9	28.7	17.4	6.3	12.7	15.1	11.6	10.9
Minimum	60.1	31.5	28.3	17.1	6.1	12.6	14.8	11.1	10.8
Maximum	66.1	32.3	29.0	17.6	6.6	13.0	15.5	12.0	11.1
±SE	±1.03	±0.13	±0.12	±0.11	±0.08	±0.08	±0.12	±0.15	±0.06
<i>Brachyphylla cavernarum cavernarum</i> (females)									
N	4	4	4	4	4	4	4	4	4
Mean	64.0	31.8	28.5	17.2	6.3	12.5	14.9	11.6	10.9
Minimum	62.6	31.4	28.2	17.0	6.2	12.1	14.7	11.4	10.8
Maximum	65.8	32.1	28.6	17.4	6.5	12.8	15.0	12.0	11.1
±SE	±0.73	±0.17	±0.10	±0.09	±0.07	±0.15	±0.09	±0.14	±0.06
<i>Monophyllus plethodon luciae</i> (males)									
N	7	8	8	8	8	8	—	8	8
Mean	42.7	23.5	22.0	10.3	4.6	9.4	—	5.6	8.1
Minimum	41.0	22.8	21.3	10.1	4.4	9.2	—	5.4	7.9
Maximum	45.6	24.1	22.4	10.7	4.8	9.7	—	5.7	8.4
<i>Monophyllus plethodon luciae</i> (females)									
N	12	11	11	11	11	11	—	10	10
Mean	41.8	23.1	21.8	9.7	4.6	9.4	—	5.4	8.2
Minimum	40.7	22.8	21.3	9.2	4.4	9.0	—	5.3	7.9
Maximum	43.6	23.5	22.1	10.1	4.8	9.7	—	5.5	8.4
<i>Artibeus jamaicensis jamaicensis</i> (males)									
N	10	10	10	10	10	10	10	10	10
Mean	59.9	29.2	26.0	17.8	7.1	12.5	15.4	12.9	10.2
Minimum	57.7	28.0	25.2	17.3	6.8	12.2	14.9	12.3	9.8
Maximum	62.2	30.2	26.7	18.5	7.4	12.9	16.0	13.4	10.7
±SE	±0.48	±0.19	±0.18	±0.12	±0.05	±0.07	±0.11	±0.10	±0.10
<i>Artibeus jamaicensis jamaicensis</i> (females)									
N	10	10	10	10	10	10	10	10	10
Mean	60.9	29.3	26.1	17.7	7.2	12.5	15.2	13.0	10.1
Minimum	58.5	28.5	25.2	17.0	6.9	12.2	14.8	12.5	9.7
Maximum	64.3	30.0	27.0	18.5	7.6	13.2	15.6	13.6	10.3
±SE	±0.51	±0.17	±0.17	±0.16	±0.09	±0.10	±0.08	±0.10	±0.06
<i>Ardops nichollsi nichollsi</i> (males)									
N	5	5	5	5	5	5	5	5	5
Mean	43.6	21.4	18.3	13.9	5.6	9.8	11.6	8.8	6.5
Minimum	42.6	20.9	17.7	13.5	5.4	9.7	11.3	8.6	6.1

Table 3.—cont.

Maximum ±SE	44.3 ±0.30	21.7 ±0.16	18.6 ±0.17	14.2 ±0.13	5.9 ±0.09	10.0 ±0.05	11.9 ±0.12	9.1 ±0.09	6.7 ±0.10
<i>Arlops nichollsi nichollsi</i> (females)									
N	6	6	6	6	6	6	6	6	6
Mean	45.9	22.2	19.3	14.5	5.6	10.0	11.9	9.5	7.1
Minimum	44.8	21.8	18.8	14.2	5.4	9.7	11.8	9.3	6.9
Maximum	47.2	22.5	19.6	14.8	5.9	10.2	12.1	9.8	7.4
±SE	±0.39	±0.12	±0.13	±0.10	±0.09	±0.09	±0.05	±0.07	±0.08
<i>Sturnira lilium angeli</i> (males)									
N	10	10	3	10	10	7	3	10	7
Mean	43.4	23.1	21.0	13.1	6.0	10.0	11.9	8.0	6.7
Minimum	42.0	22.5	20.7	12.7	5.7	9.8	11.5	7.8	6.1
Maximum	45.2	23.7	21.2	13.5	6.4	10.2	12.1	8.3	7.4
±SE	±0.36	±0.12	±0.15	±0.07	±0.08	±0.06	±0.19	±0.06	±0.16
<i>Sturnira lilium angeli</i> (females)									
N	10	10	10	10	10	10	10	10	10
Mean	44.2	23.1	20.9	13.0	5.7	9.9	11.7	8.1	6.5
Minimum	43.6	22.8	20.5	12.7	5.4	9.6	11.2	8.0	6.2
Maximum	44.9	23.4	21.3	13.3	5.9	10.4	11.8	8.4	6.6
±SE	±0.19	±0.06	±0.08	±0.07	±0.05	±0.07	±0.06	±0.05	±0.04

Weights of the females taken in the spring of 1966 show a close relationship with pregnancy. The three females mentioned above in advanced stages of pregnancy weighed 50.9, 57.5, and 62.0, respectively. Eight males collected in the same period averaged 44.6 (39.7 to 48.4) in weight.

A single adult female *Brachyphylla* was checked for rectal temperature. This bat, in a relatively quiet state after being removed from a bat net, had a temperature of 37.5°C.

An adult male obtained on April 23, 1966, showed evidence of molt, which appears to be the result of gradual replacement of old pelage by new, with little loss of old hairs at any single spot. This bat (KU 104797) had a mottled dorsum, especially posteriorly, where pelage had been shed after new hairs had become well established. New pelage is present over the dorsum (except on the head anterior to the ears), although in most areas many old hairs still are present; there was no gross evidence of molt on the venter.

Ectoparasites collected from individuals of *B. c. cavernarum* included batflies, *Trichobius truncatus* Kessel, which were taken from 11 of 12 specimens examined on Dominica. One male was parasitized by 26 batflies. This streblid also was taken from *Monophyllus plethodon luciae*. Wing mites of the family Spinturnicidae also were found on *Brachyphylla*.

Monophyllus plethodon luciae Miller
Antillean Long-tongued Bat

Specimens examined (63).—ST. ANDREW PARISH: Marigot, 100 ft, 1 (KU 104765). ST. JOSEPH PARISH: Clarke Hall Estate, 100 ft [=30 m], 27 (KU 104766-79, TTU 9337, 31330-31, 31334-40, NMNH 361896, 391225, 391272); 1 mi. above mouth Layou River, 5 m, 1 (TTU 31332); York Valley Estate, 2 (TTU 63353-54). ST. PAUL PARISH: 1.5 mi. NW Mahaut, sea level, 1 (KU 104780); 0.5 mi. NE Mt. Joy, 2000 ft, 1 (TTU 62223); Mt. Joy Estate, 3 (TTU 63355-57); 1/4 mi. NE Pont Cassé, 2500 ft, 18 (TTU 62224-41); 6 mi. NE Roseau, 1100 ft, 1 (KU 151216); Spring-

field, 6 (TTU 31329, 31333, 31341-44); Sylvania, ca. 1700 ft, 2 (NMNH 361897, 362096).

Additional records.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985). PARISH UNKNOWN: "Dominica" (Koopman, 1968:3--specimen originally reported by Howes, 1930:101).

Remarks.—Schwartz and Jones (1967) reviewed the genus *Monophyllus*, reduced the number of recognized species from six to two (*redmani* and *plethodon*), and referred specimens from Dominica to the subspecies *M. p. luciae*. From the nominate subspecies, *M. p. plethodon* of Barbados, *luciae* differs only in being slightly larger, and is tentatively recognized until additional comparative material of the rare Barbadian race is available for study.

Monophyllus plethodon luciae is distributed in the Lesser Antilles from Anguilla southward to St. Vincent. Other subspecies occur on Barbados and on Puerto Rico where it is known only from fossil remains. The long-tongued bat was first reported from Dominica by Howes (1930), but his account was overlooked by most subsequent authors. The occurrence of this species on the island came to light only after field parties operating under the aegis of the Bredin-Archbold-Smithsonian survey obtained additional specimens there in the period 1964 through 1966. *M. plethodon* evidently is widely distributed and not uncommon on the island.

Comparison of measurements of males and females from Dominica (Table 3) indicates there may be secondary sexual dimorphism in this genus, at least on Dominica, in that males average larger than females in external and four cranial measurements. However, these differences may result from the small sample available for study. Two females are markedly paler than the normal dark brownish coloration of *M. p. luciae*; both (KU 104779, NMNH 361897) are a pale buffy tan. Schwartz and Jones (1967:14) proposed two possible explanations for this variation in color, however, until more extensive material is available the exact nature will remain unknown. No noteworthy variation was found in the dentition.

Twenty-seven of the long-tongued bats examined from Dominica were captured in mist nets at Clarke

Hall Estate in March of 1964, December of 1965, March and April of 1966, and July 1978. These were taken in the following situations: in a grapefruit orchard; above a trail separating a cocoa planting from a row of trees; over a bar in the Layou River in a net that was set from the wooded border of the stream bed part way across the river; and in a banana-coconut grove adjacent to the Layou. Nets placed in these same areas (in three instances the exact place where specimens had been netted in 1966) in September of 1967 failed to capture *M. plethodon*. *Monophyllus* was taken in the same nets at Clarke Hall with *Ardops*, *Artibeus*, *Brachyphylla*, *Sturnira*, and *Myotis*. As many long-tongued bats were netted after 2300 at night as before that time, possibly indicating that this species forages throughout much of the night.

Aside from Clarke Hall Estate, *Monophyllus* has been taken at 10 other localities on Dominica. On April 12, 1966, a mummified male was found 1-1/2 mi. NW Mahaut at the entrance to a small cave located in rocks facing on the Caribbean beach. No other bats were found in the cave although an adjacent larger cave harbored *Tadarida brasiliensis* and *Artibeus jamaicensis*. On April 16, 1966, one *Monophyllus* was taken in a mist net placed in a banana grove at Marigot. It was the only bat taken in this net. A single female was netted in a clearing in thick forest at Sylvania on March 3, 1964, whereas one from 6 mi. NE Roseau was taken in a net stretched across a mountain stream. At Springfield Estate (Fig. 2) two Antillean long-tongued bats were taken on the night of July 19, 1978, in nets set across a fly-way leading up from a small river toward the estate buildings and on the night of July 23 four additional *M. plethodon* were taken in nets set under rows of mango trees. On the evening of July 21, a single long-tongued bat was captured in a mist-net set under a row of mango trees that separated cacao groves about a mile above the mouth of the Layou River. Two *Monophyllus* were netted at the York Valley Estate on the night of June 26, 1992, in an area with mixed vegetation including new banana groves, an old citrus orchard, and some native forest. The two long-tongued bats were taken between 2200 and 2300 hours. Two additional specimens were netted near the headquarters of Mt. Joy Estate on the evening of June 29, 1992, before 2300 hours.

Long-tongued bats have been reported as cave inhabitants on several Antillean islands, but are not among species that have been taken in caves on Dominica. Schwartz and Jones (1967:14) assumed, evidently incorrectly, that a specimen earlier listed from Dominica by Howes (1930:101) had been taken in a cave.

Eight of nine females taken on Dominica from March 24 through April 22, 1966, were pregnant, all with a single embryo. The nongravid female was taken on March 24. A female taken on March 28, 1964, was also pregnant, but one captured on December 4, 1965, was not. Embryos ranged in size from 17 to 18 from March 24 to 27, 18 on April 9, and 20 to 24 from April 16 to 22. A female taken July 25, 1978, at Clarke Hall Estate was carrying a single embryo that measured 20; however, eight additional females taken that night were nongravid, as were three females taken at Springfield on July 20 and 24. Testes of six males

measured from 4 to 4.5 in length in late March and April of 1966, 2 in a single male taken June 28, 1992, and 5 and 3 in males taken on July 22 and 24, 1978, respectively. Pregnant females weighed from 14.3 to 17.0, with the weight dependent on embryo size; six non-pregnant females weighed on average 13.2 (12.5–14.0). Eight males ranged in weight from 13.8 to 17.2.

Rectal temperatures obtained from a *Monophyllus* on March 28, 1966, showed an increase from quiescence to active state of almost 5°C in five minutes. The bat was held in a collecting bag overnight before the temperatures were taken. The first reading (30.5°C) was taken directly upon removal of the quiescent bat from the bag, the last reading (35.2°C) after rigorous non-flying activity.

Ectoparasites found on *Monophyllus* included *Nycterophilia coxata* Ferris and *Trichobius truncatus* Kessel, batflies of the dipteran family Streblidae.



Figure 2. View of the Springfield Estate, St. Paul Parish, Dominica.

Monophyllus was the only Dominican bat from which *N. coxata* was obtained. Mites of the family Spinturnicidae, not identified to species, also were found.

Artibeus jamaicensis jamaicensis Leach
Jamaican Fruit-eating Bat

Specimens examined (188).—ST. GEORGE PARISH: Trafalgar Falls, 4 mi. NE Roseau, 1000 ft, 1 (KU 104908); Roseau, 2 (TCWC 55717-18); Botanic Garden, Roseau, 50 ft, 1 (KU 104909). ST. JOHN PARISH: 1 mi. NW Portsmouth, 100 ft, 2 (KU 104815-16). ST. JOSEPH PARISH: Clarke Hall Estate, 100 ft, 96 (KU 104817-902, 110157-58, NMNH 362098, 391276-82); York Valley Estate, 1 (TTU 63358). ST. LUKE PARISH: South Chiltern Estate, ca. 1300 ft, 3 (NMNH 361902-03, 391234). ST. PATRICK PARISH: Grand Bay, 50 ft, 10 (KU 104910-19). ST. PAUL PARISH: 0.5 km S Canefield, 7 (TTU 63359-65); 2.5 mi. S Layou [*in* St. Joseph Parish], 5 (KU 151354-58); 1 1/2 mi. NW Mahaut (some specimens from this locality are labeled as from Rodney's Rock), sea level, 13 (KU 104903, NMNH 361900-01, 361904, 362099, 391226-33); Massacre, sea level, 4 (KU 104904-07); Mt. Joy Estate, 3 (TTU 63366-68); 6 mi. NE Roseau, 1100 ft, 14 (KU 151359-72); Springfield, 25 (TCWC 55719-22, TTU 31362-82). PARISH UNKNOWN: "Dominica," 1 (NMNH 113628).

Additional record.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985).

Remarks.—The nominate subspecies *Artibeus jamaicensis jamaicensis* is distributed from Jamaica eastward through Hispaniola and Puerto Rico, thence southward through the Lesser Antilles to St. Lucia and Barbados. It is a common inhabitant of most islands and is one of the most widely distributed and conspicuous species on Dominica.

Andersen (1906:421), in the original description of *Artibeus jamaicensis praeceps* (the first report of this species from Dominica), and later in his monograph of the genus *Artibeus* (1908:283), compared *praeceps* to *A. j. palmarum* [= *Artibeus lituratus palmarum*] and stated that *praeceps* was indistinguish-

able from the latter except for being smaller in size, especially forearm and metacarpals. Later, Hershkovitz (1949:447) allocated Dominican *Artibeus* to the species *lituratus*, based principally on Andersen's earlier remarks. However, Dominican specimens do not possess the characters typical of *A. lituratus*, which occurs in South and Central America, the tropics of Mexico, and in the southern Windward islands (north to St. Vincent). The uropatagium, for example, is much less pilose, the forearm averages considerably shorter than in *lituratus*, and the postorbital process is much less pronounced (shallower orbital ridges). Furthermore, the interorbital breadth is narrower in *A. lituratus* than in *A. jamaicensis* and the nasals are broader. The pelage of Dominican specimens varies from grayish though grayish brown to brownish and the facial stripes are usually indistinct. Clearly, Dominican *Artibeus* are referable to the species *jamaicensis*, and as shown below to the subspecies *A. j. jamaicensis*.

Specimens of the Jamaican fruit-eating bat from Cuba south through Trinidad (Table 4) were reviewed with reference to variation in size and presence or absence of the third molar in both jaws. Specimens from Cuba and the Bahamas to which the subspecific name *parvipes* is applicable, are smaller, both externally and cranially, than are those from Jamaica south to Dominica and beyond (Table 4). A comparison of specimens from Jamaica southward to Dominica revealed no significant differences in external or cranial dimensions. Thus, the Dominican specimens are appropriately referred to the nominate subspecies, of which *praeceps* is a junior synonym. Bats from St. Vincent are much larger in size (Jones, 1978) than any other population in the West Indies and have been assigned to the subspecies *A. j. schwartzi*. Genoways et al. (1998) presented the reasons for assigning Grenadan populations to *A. j. grenadensis*, and for restricting island populations of *A. j. trinitatis* to Trinidad and Tobago. Genetic data presented by Phillips et al. (1989) and Pumo et al. (1996) also support this subspecific arrangement for Antillean populations of *A. jamaicensis*.

Further evidence for this subspecific arrangement and for the zoogeographic affinities of Antillean *A. jamaicensis* are shown by the incidence of presence or absence of the third upper molars (Table 4).

Specimens examined from Dominica and islands to the north lack the M3, whereas individuals from Grenada and Trinidad generally possess these teeth as do *jamaicensis* from the adjacent mainland of South America. Thus, there appears to be a break in the distribution of *Artibeus jamaicensis* in the Lesser Antilles. Bats from Grenada and Trinidad are related to South American mainland populations, whereas the northern Antillean *Artibeus* evidently are more closely related to populations from the Yucatan Peninsula and elsewhere in adjacent Middle America, which also lack the upper third molar. Geographic variation in the presence of M3 is known to occur also in *A. jamaicensis* in Middle America and in South America (Handley, 1966:299). In addition to the absence of the third upper molars in specimens from the northern part of the Lesser Antilles, there is some variation in these same individuals in the presence of the third lower molars (Table 4).

Some variation exists in size and spacing in the dentition in specimens from Dominica. The upper incisors usually are slightly imbricate in adults, but an adult female (KU 151360) from 6 miles NE Roseau exhibits an extremely wide spacing of incisors. The lower third molars of specimens studied varied in size from a small, peglike tooth to relatively large tooth with definite cuspidate patterns. Two specimens of *A. j. jamaicensis* examined from Dominica possessed supernumerary teeth, both cases occurring in lower dentition. An adult male (KU 104885) has a small, extra second lower incisor on the left side, situated to the inside of the normal incisor, which is slightly crowded forward. Another adult male (KU 104891) possesses a supernumerary lower right premolar, which is located between the two normal-sized premolars; the extra tooth, reduced in size, resembles the first premolar. Generally speaking, variation in dental morphology is not unusual in these fruit bats. An adult female (KU 151355) obtained on March 26, 1961, at a place 2 1/2 miles south of Layou appears to have had a broken right mandible. The fracture, between the outer incisors and the canine, caused no unusual wear on the dentition, possibly occurred while the bat was young, and healed with no visible ill effects to the bat.

An analysis of specimens from Dominica reveals no significant secondary sexual variation in external and cranial features (Table 3).

Some variation in color of pelage exists, but the color varies independently from sex. Older animals vary in color from brownish to grayish dorsally, brownish being predominant, and in the same manner ventrally except that ventral hairs are tipped with grayish white. Immature bats have short, soft, gray pelage. Young adults have grayer pelage than do older animals, even after the first molt. The distinctness and color of facial stripes varies greatly between individuals, independent of sex. Animals with grayish fur generally have facial stripes that are whitish in color, whereas those bats with brownish fur have stripes that are more or less tan. The clarity and darkness of the stripes varies independently from fur color.

Artibeus jamaicensis is one of the most abundant bats on the island of Dominica. It has been collected there in all months except October, leaving no doubt that the species is a common resident at all seasons. The species was taken in nets set in a variety of habitats. Near Clarke Hall Estate, for example, fruit-eating bats were taken in mist nets set across the Layou River, in coconut groves and banana groves, and among trees and shrubs lining the trails adjacent to cocoa plantations. The following kinds of bats were taken in association with *A. jamaicensis* at Clarke Hall: *Ardops nichollii*, *Brachyphylla cavernarum*, *Monophyllus plethodon*, *Sturnira lilium*, and *Myotis dominicensis*.

Artibeus jamaicensis also was collected in caves: for example, individuals were shot from a small colony in a sea cave located just north of Massacre on March 25 and females and young were taken from a maternity colony in a man-made cave located behind the Catholic Church at Berekoa, about 50 feet above Grand Bay, on April 7. On April 12 a single female was taken from a small maternity colony in a sea cave situated 1 1/2 mi. NW Mahaut. Other known circumstances of capture reveal two specimens taken along with one *Ardops nichollii* on April 2 in a net stretched along a trail leading to the ruins at the "Cabrit," on the northwest point of the island; a single female netted adjacent to Trafalgar Falls, 4 mi. NE Roseau, on April 6 (Fig. 3); several individuals netted along with one *Ardops nichollii* at a pond in the Botanic Garden at Roseau on April 14; a sample of 21 individuals taken on the evening of July 19, 1978, in nets set under a mango tree on the Springfield Estate; and 10 individuals of which one was preserved, captured on the night

Table 4.—Variation in selected measurements of *Artibeus jamaicensis* from certain Antillean islands (arranged from north to south). Percent of occurrence of both upper and lower third molars is also given.

Subspecies and island	Forearm	Greatest length skull		Breadth across M3-M3		Percent m3 present* (N)
	Mean (range) N	Mean (range) N	Mean (range) N	Mean (range) N		
<i>Artibeus jamaicensis parvipes</i>						
Bahamas	56.3 (52.7-59.8) 20	27.3 (26.5-27.5) 6	11.9 (11.6-12.2) 6	0 (6)	83 (6)	
Cuba	56.4 (54.5-58.0) 20	26.7 (26.0-28.3) 20	11.6 (11.0-12.7) 20	0 (81)	98 (80)	
<i>Artibeus jamaicensis jamaicensis</i>						
Jamaica	58.9 (54.6-62.1) 20	28.2 (27.1-29.3) 10	12.3 (12.1-12.8) 11	0 (11)	100 (11)	
Hispaniola	58.1 (54.7-60.9) 18	28.0 (27.0-28.6) 17	12.3 (11.9-12.7) 18	0 (33)	95 (20)	
Puerto Rico	60.2 (58.0-62.9) 20	28.5 (27.7-29.4) 20	12.7 (12.3-13.1) 20	0 (61)	92 (63)	
St. John	59.0 (57.2-61.2) 20	28.3 (26.8-29.5) 20	12.4 (12.0-12.8) 20	0 (45)	89 (45)	
Dominica	60.2 (55.6-64.7) 89	29.1 (28.0-30.6) 87	12.9 (12.1-13.7) 91	0 (97)	94 (97)	
<i>Artibeus jamaicensis schauinslandi</i>						
St. Vincent	63.6 (62.1-64.6) 8	30.9 (30.1-31.8) 8	14.1 (13.5-14.7) 8	39 (10) ^{1***}		
<i>Artibeus jamaicensis grenadensis</i>						
Grenada	58.3 (52.5-61.6) 17	28.5 (26.9-29.2) 17	12.8 (12.3-13.6) 18	89 (18) ^{**}	100 (18)	
<i>Artibeus jamaicensis trinitatis</i>						
Trinidad	57.6 (55.2-60.9) 17	28.3 (26.2-28.1) 6	12.1 (11.6-12.5) 7	100 (8)	100 (8)	

*Considered as "absent" if one of pair missing.

**Two specimens possess M3 missing on only one side.

¹Data from Jones (1978).

of June 26, 1992, in an area characterized by newly planted bananas, an old citrus orchard, and native forest on the York Valley Estate. Normal weather conditions do not appear to affect the activity of *A. jamaicensis*, inasmuch as these bats were active on clear nights as well as cloudy or rainy nights.

Residents of the island reported that these bats frequently ate young coconuts, but no evidence of such activity was found by investigators associated with the Bredin-Archbold-Smithsonian parties. Figs were the only fruits found in and below nets in which *A. jamaicensis* was taken.

Rectal temperatures were recorded on both sexes of *A. jamaicensis* from Dominica in normally active states. Three females examined averaged 37.9°C

(36.6°C to 39.9°C), whereas eight males averaged 38.4°C (37.8°C to 39.2°C). Four quiescent males, retained overnight in a collecting bag, had temperatures slightly lower than did active males averaging 36.4°C (34.7°C to 37.7°C). In another instance, an active female showed a rise from 35.6°C to 36.4°C within a few minutes.

Reproductive data, collected during part of the spring dry season and also in the wet season of summer, are tabulated in Table 5. In addition to the data presented in Table 5, a female taken on March 24, 1964, was pregnant as were single females obtained on April 1, April 6, and April 16 in the same year. Two females collected on January 31 and six collected in late November and early December revealed no gross reproductive activity. These reproductive data appear



Figure 3. Trafalgar Falls, 4 miles [6.5 kilometers] northeast of Roseau, St. George Parish, Dominica. The elevation is 1000 feet [=305 meters].

to follow the same pattern as reported for the species in other areas of its geographic range, where it exhibits bimodal polyestry (Wilson, 1979; Wilson et al., 1991). Females are palpably pregnant in January, give birth in late February and March, and again are palpably pregnant in April, May, or June with births in July and August. Only 50% of females in our sample were pregnant in late March, but by April and again in July more than 70% of females were pregnant (Table 5). By late August and early September, most females had given birth, but were still lactating. Individuals taken in November and December were not reproducing as would be expected elsewhere in this species.

Reproductive activity in males also was recorded in 1966, 1967, 1978, and 1992. Two males had testes measuring 9.5 to 10 during late March; seven examined in early April had testes averaging 8.7 (7 to 11), and in late April three males all had testes measuring 8. Five males taken on June 26 of 1992 had testes that averaged 10 (8-12) in length. An individual taken on July 9 of the same year had testes measuring 11. Six males captured between July 19 and 21, 1978, had testes lengths that were on the average 8.1 (6-10). In late August and early September of 1967, 10 males averaged 8.5 (4 to 11) in testicular length.

Males average lighter in weight than non-pregnant females. Fifteen males averaged 41.3 (36.3 to 46.2), whereas 15 non-pregnant females had an average weight of 44.8 (38.2 to 50.2). The weight of gravid females is directly correlated with stage of de-

velopment of the embryo; 12 gravid females averaged 47.9 (34.9 to 64.7); the heaviest all carried near-term embryos.

Three young were born alive to females held in collecting bags. The three (KU 104821, 104824, 104844) are covered dorsally by short, dark gray hairs. There is no visible ventral or lateral hair on the body nor is any visible on the forearms. These neonates have well-developed claws. Respective forearm measurements for the three are 28.8, 24.5, and 28.4. The first, a female born on March 25, 1966, had the following external measurements: total length, 52; length of foot, 17; length of ear, 12.5. Weights for the three specimens, respectively, were: 10.7, 9.7 (March 26, 1966), and 9.5 (March 29, 1966).

Four young bats taken on April 7, 1966, from a maternity colony in a man-made cave at Grand Bay are distinctly larger than the above-mentioned day-old young. Two (KU 104916-17), a female and male, are smaller than the other two (KU 104918-19), both females. The smaller pair are covered dorsally by a soft, short, dark pelage and ventrally with a sparse, short, pale gray pelage. The larger pair have feet and thumbs of adult size; their forearms, 51.1 and 46.3, approach the lower limit (55.6) of adults, even though these young were not yet able to fly (the phalanges are of soft cartilage and appear not yet able to support flight). A juvenile male (TTU 63359) taken on June 26, 1992, at a place 0.5 kilometer south of Canefield, had a forearm length of 49.1 and weighed 19. As the young

Table 5.—Reproductive data from female *Artibeus jamaicensis* from Dominica, spring of 1966 and summer of 1967.

Dates	Number examined	Number pregnant	Size of embryos (mm.)			Number lactating	Percent reproductively active
			5-15	16-30	31-45		
March 23-29	12	6	2	0	4*	0	50.0
April 3-13	27	11	7	0	4	15	96.3
April 18-24	28	18**	8	9	0	6	85.7
July 19-21	14	10	2	5	5***	0	71.4
August 30-September 2	13	2	1	0	1	9	84.6

*Includes three young born in collecting bags.

**Includes one female with unmeasured embryo.

***Includes one young born in collecting bag.

develop, the color of the juvenile pelage becomes paler gray and the fur becomes noticeably sparser as the surface increases with growth. The larger pair of young have longer central hairs than do the smaller pair, but the pelage still is sparse.

Judging from the day-old young, the hooked, outer upper incisors are the first elements of the deciduous dentition to appear. The next smallest young (KU 104916-17) have the hooked upper incisors and all the hooked canines present, but no lower incisors are visible. The two largest young (KU 104918-19) have the full complement of deciduous incisors and canines present and the last upper deciduous premolars also had erupted.

Evidence of molt was found on only four adult *Artibeus jamaicensis* from Dominica, and molt evidently occurs primarily as an abrupt replacement of old hairs by new. Three females (KU 104825, 104884, 104897) revealed varying degrees of ventral molt, the old pelage having disappeared in the areas where new hair was present. One lactating female (KU 104825) evidenced considerable mid-ventral molt, progressing posteriorly, but there appears to be no definite molt pattern. One female (KU 104911) exhibited considerable loss of hair—almost all the ventral pelage and a saddle-shaped patch of dorsal hair—with no obvious replacement either dorsally or ventrally. Many females, most of which were lactating, had lost hair on the chin and throat.

Two species of batflies of the family Streblidae, *Megistopoda aranea* (Coquillett) and *Aspidoptera phyllostomatis* (Perty), were taken from *Artibeus* and are known from *A. jamaicensis* elsewhere in its range. These batflies also were collected on *Sturnira lilium*. Wing mites of the family Spinturnicidae also were obtained from *A. jamaicensis*. Numbers of mites varied considerably between individual bats. The total numbers of mites found on three adult males on August 29, 1967, for example, were 146, 52, and 22 spinturnicids.

Ardops nichollsi nichollsi (Thomas)
Antillean Tree Bat

Specimens examined (19).—ST. GEORGE PARISH: Botanic Garden, Roseau, 50 ft, 1 (KU 104814). ST. JOHN PARISH: "Cabrit," NW Portsmouth, ca. 200 ft, 1 (NMNH 361905); 1 mi. above mouth Layou River, 3 (TTU 31359-61); 1 mi. NW Portsmouth, 100 ft, 1 (KU 104804). ST. JOSEPH PARISH: Clarke Hall Estate, 100 ft [=30 m], 11 (KU 104805-11, 1048163, TTU 9341, 31357-58). ST. PAUL PARISH: 6 mi. NE Roseau, 1100 ft, 1 (KU 152362). PARISH UNKNOWN: Dominica, 1 (MCZ 16446).

Additional record.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985).

Remarks.—The subspecies *Ardops nichollsi nichollsi* is restricted in distribution to Dominica and was the first species of bat reported from the island. Thomas (1891:530) in his description of the species reported the locality only as "Island of Dominica, West Indies." The monotypic genus *Ardops*, revised by Jones and Schwartz (1967), is known also from St. Eustatius, Montserrat, Guadeloupe, Martinique, St. Lucia, and St. Vincent (Jones, 1989).

The nominate subspecies of *Ardops nichollsi* on Dominica is the smallest of the named races in the Antilles. In comparing individuals from different islands, Jones and Schwartz (1967) found no geographic clinal relationship to size, but rather that variation was island-specific. Four kinds formerly recognized as monotypic species were thus arranged by them as subspecies of *Ardops nichollsi*.

Ardops nichollsi nichollsi exhibits marked secondary sexual dimorphism on Dominica (Jones and Schwartz, 1967). Males are significantly smaller than females in all but two of the characters (postorbital constriction in which the means are the same and breadth of braincase in which males do average smaller) shown in Table 3. Of the seven remaining characters,

there is no overlap in the range of measurements of the sexes in five, including breadth across upper molars and length of the maxillary toothrow, which differ at the $P \leq 0.001$ level, and length of forearm, greatest length of skull, and condylobasal length, which differ at $P \leq 0.01$ level (Table 3). Zygomatic breadth of males and females overlaps at 14.2 ($P \leq 0.01$) and mastoid breadth overlaps at 11.8 and 11.9 ($P \leq 0.05$). Color varies individually from dark brown to yellowish brown, but does not differ between the sexes.

On March 3, 1964, a female was netted near the ruins of the old fort (Cabrit) on Prince Rupert Bluff (Fig. 4), and a female was taken near there on April 2, 1966, in a net set across a trail through dry, scrubby forest bordering the western edge of the island. A female was trapped at Clarke Hall Estate on March 27, together with *Artibeus*, *Monophyllus*, and *Myotis*, in a net stretched across a trail bordered by trees and a cocoa grove; a net across a rock-gravel bar, bordered by vegetation, in the Layou River at Clarke Hall captured eight *Ardops*, along with representatives of the genera *Artibeus*, *Brachyphylla*, *Monophyllus*, and *Sturnira*, in late March and mid-April. One *A. nichollsi* was netted at the edge of a pond in the Botanic Garden

at Roseau on April 14, 1966, along with *Artibeus jamaicensis*, whereas a male from 6 miles northeast of Roseau was taken in a net set over a stream in a rain forest along with *Artibeus*, *Brachyphylla*, *Monophyllus*, *Sturnira*, *Natalus*, and *Tadarida*. Interestingly, nets set at Clarke Hall in late August and early September of 1967 failed to capture *Ardops*, even though some were strung in exactly the places where these bats had been taken in 1966; however, nets set on the evening of July 24, 1978, in this place took two *Ardops* as well as representatives of *Artibeus*, *Monophyllus*, and *Sturnira*. This suggests that these bats may be moving seasonally between different habitats on the island.

Most bats of this species netted in 1966 were captured between darkness and 2200, but several were taken after midnight. Four quiescent bats, of which three were female, had rectal temperatures averaging 35.9°C (32.6°C to 37.4°C). A single active female had a rectal temperature of 37.8°C . Five males weighed an average of 16.9 (15.1-18.5); two non-pregnant females weighed 18.3 and 18.7 (lactating), whereas four pregnant females averaged 22.8 (17.8-25.2).



Figure 4.—Cabrits Peninsula, St. John Parish, on the northwestern coast of Dominica.

All five females taken in the spring of 1966 were reproductively active. Four carried a single embryo on the following dates (crown-rump length in parenthesis): March 27 (11); March 28 (21); March 29 (31, near term); and April 14 (29, near term). A female taken on April 19 was lactating. A female handled on July 25, 1978, carried a single embryo measuring 32 in crown-rump length. Males taken in late March and April had testes measuring 4.5 to 6.0, whereas four males taken on July 22 and 25, 1978, all had testes measuring 5 in length.

No batflies were found on *Ardops*. Wing mites of the family Spinturnicidae and hair mites of the family Listrophoridae were collected.

Sturnira lilium angeli de la Torre
Yellow-shouldered Bat

Specimens examined (62).—ST. JOSEPH PARISH: Clarke Hall Estate, 100 ft, 25 (KU 104781-91, 110121-33, TTU 31404); 1 mi. above mouth Layou River, 5 m, 2 (TTU 31405-06); York Valley Estate, 2 (TTU 63369-70). ST. PAUL PARISH: 0.5 mi. NE Mt. Joy, 2000 ft, 1 (TTU 62242); Mt. Joy Estate, 4 (TTU 63371-74); 1/4 mi. NE Pont Cassé, 2500 ft, 1 (TTU 62243); 6 mi. NE Roseau, 1000 ft, 6 (KU 151322-26, NMNH 361881); Springfield, 21 (TCWC 55723-25, TTU 31407-24).

Additional records.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985). PARISH UNKNOWN: "Dominica" (de la Torre, 1966:272, see also Koopman, 1968:4).

Remarks.—*Sturnira lilium angeli*, as currently understood, is known only from Dominica. Formerly this species was considered uncommon on Dominica, but continued collecting has shown that it is fairly abundant in suitable habitats. A. H. Verrill collected the first specimens of *Sturnira* on Dominica in 1906 (Allen, 1911:233). Subsequently, Albert Schwartz and associates obtained six individuals there in 1962. In 1966 and 1967, J. Knox Jones, Jr., and Carleton J. Phillips collected 24 additional specimens on the island and Karl F. Koopman also obtained two in 1967. In 1978, Jones along with Robert J. Baker added 21 specimens to collections. Robert Owen and his student took 8

specimens in 1991-92 and in the same time period Keith Arnold, David Slack, and their students captured three *S. lilium*. Hill and Evans did not report the number of specimens of the yellow-shouldered bats that were taken at Syndicate so we only are able to document that a minimum of 66 specimens of this species are now known from Dominica, which is more specimens of this species than are known from all other Lesser Antillean islands combined.

Bats of the genus *Sturnira* are now known in the Lesser Antilles from Montserrat (Pedersen et al., 1996; Genoways, 1998) southward to Grenada (Genoways, 1998; Genoways et al., 1998), but are unreported from Barbados and the Grenadines (Jones and Phillips, 1976). Two species with seven subspecies are recognized in the region (de la Torre, 1966; de la Torre and Schwartz, 1966), but subsequent to the work of Jones and Phillips (1976) these taxa have been assigned as subspecies to the widespread mainland species *Sturnira lilium*. On Guadeloupe, just off the north of Dominica, a separate species, *S. thomasi*, is recognized. It has been considered a distinct species by all recent authors based upon its relatively large size and long and narrow skull (Genoways and Jones, 1975; Jones and Phillips, 1976; Baker et al., 1978; Jones, 1989; Koopman, 1989; Pedersen et al., 1996; Genoways, 1998). We believe that this arrangement is appropriate because we see no tendency in our specimens from Dominica toward the characteristics of *S. thomasi*.

The sample of *Sturnira* from Dominica was examined for secondary sexual variation (Table 3). Males were significantly larger than females in breadth of the postorbital constriction ($P \leq 0.01$) and females were significantly larger in length of forearm ($P \leq 0.05$). In the remaining seven measurements, there were no significant differences and the means did not differ by more than 0.2 mm.

Individuals of *Sturnira* netted on Dominica were most often taken in nets placed across trails through forest or plantings, or over streams. In 1966, *Sturnira* was captured in nets along with *Ardops nichollsi*, *Artibeus jamaicensis*, *Brachyphylla cavernarum*, *Monophyllus plethodon*, and *Myotis dominicensis*. In 1967, only *Artibeus* and *Sturnira* were taken together. Specimens were taken on clear as well as cloudy and rainy nights, and were captured both early and late in

the night. De la Torre (1966:272) recorded *Artibeus*, *Brachyphylla*, and *Sturnira* as taken together in nets over streams in rain forest in the vicinity of Roseau.

All 11 yellow-shouldered bats collected in March and April of 1966 were gravid females, each with a single embryo. Between March 22 and April 4, eight embryos ranged from 16 to 24 (average 20.5); three embryos obtained between April 10 and 22 averaged 25.6 (22 to 28). Two of three females taken between June 2 and 13 were lactating, but the third evinced no reproductive data, whereas three adult females taken on the evening of June 30 were pregnant, containing embryos measuring 18, 19, and 20. A female taken on the night of July 20 carried a single embryo measuring 18. Only one (lactating) of four females taken in late August and early September of 1967 evidenced reproductive activity. Testes of eight males taken in this same period averaged 4.7 (2.5 to 7), whereas three males taken on July 20 and 22 had testes averaging 5.3 (3-7). Weights of eight gravid females taken in March and April ranged from 21.1 to 24.7 (average 22.5), whereas three pregnant females captured in late June weighed 20, 21, and 23. A non-pregnant female taken on June 2 weighed 22 and a lactating female taken on June 13 weighed 21.5.

Two flying subadult females (TTU 63369-70) were netted on the night of June 27 at the York Valley Estate. These individuals had forearms that measured 42.0 and 41.9 in length and weighed 13 and 12, respectively. On July 1, a single subadult female was netted along with three pregnant female yellow-shouldered bats. The subadult weighed 18 as compared with the lightest adult at 20 and had a length of forearm of 43.5 as compared with the lightest adult at 20 and had a length of forearm of 43.5 as compared with the adult females with 41.8, 42.4, and 43.0. At Springfield on July 20, a flying subadult male with a forearm length similar to those of the adults at 42.9 was captured in a mist net. Although our reproductive data are not extensive, the pattern of reproduction for this Antillean population is not inconsistent with the bimodal polyestry model suggested by Wilson (1979) for mainland populations of yellow-shouldered bats.

Rectal temperatures were recorded for six adult yellow-shouldered bats taken in the late summer of 1967. A quiescent female had a temperature of 34.2°C;

the temperature of this bat was the same when tested again in a half-hour. An active female had a rectal temperature of 37.0°C, whereas four active males averaged 34.9°C, with extremes of 31.9°C to 37.9°C.

A male collected on August 30, 1967, exhibited variation in pigmentation of the wings not seen in other specimens of *S. lilium* in that the tips of each wing were white.

Batflies of the dipteran family Streblidae found on *Sturnira lilium angeli* were *Aspidoptera phyllostomatis* (Perty), *Megistopoda aranea* (Coquillett), and *Metelasmus pseudopterus* Coquillett. *M. pseudopterus* was found only on *S. l. angeli*, but the first two species of batflies also were taken from *Artibeus jamaicensis*. Wing mites of the family Spinturnicidae also were taken from *S. l. angeli*.

Family NATALIDAE

Natalus stramineus stramineus Gray Funnel-eared Bat

Specimens examined (97).—ST. GEORGE PARISH: 6 mi. NE Roseau, 1100 ft, 1 (KU 150726); Trafalgar Falls, 1000 ft, 4 mi. NE Roseau, 11 (KU 104920-30); Roseau, ca. 50 ft, 1 (NMNH 113185). ST. JOHN PARISH: Tanetane, 33 (NMNH 361906-10, 361946-54, 362100-04, 391235-48); 0.5 mi. N Toucari, 100 m, 29 (TTU 31457-85). ST. PAUL PARISH: Springfield, 1 (TTU 31486). PARISH UNKNOWN: "Dominica," 21 (MCZ 17781, NMNH 62850, 113596-614).

Additional record.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985).

Remarks.—There have been conflicting opinions on the specific relationships of populations of funnel-eared bats in the Lesser Antilles, Greater Antilles, and on the mainland of Mexico and Central America. Arroyo-Cabrales et al. (1997) have recently examined this problem using allozymic data. Although their data gave only minimal resolution to this systematic question, they concluded that work by earlier authors (Varona, 1974; Hall, 1981; Koopman, 1993) indicating

that the mainland and insular populations of this group represent a single species—*Natalus stramineus*--was the appropriate conclusion.

The nominate subspecies of funnel-eared bat is known in the Lesser Antillean region only from seemingly isolated populations on six islands (Anguilla, Saba, Antigua, Montserrat, Guadeloupe, and Dominica) in the northern part of the Lesser Antilles (Jones, 1989). Other subspecies of *Natalus stramineus* occur on the Greater Antillean islands of Jamaica (*jamaicensis*), Hispaniola (*major*), and Cuba (*primus*, fossil only), whereas on Trinidad to the south of Dominica is another, considerably smaller, species, *N. tumidirostris* (Varona, 1974; Carter et al., 1981). On Dominica, *N. s. stramineus* evidently is locally common in areas having appropriate roosting sites.

This species was first reported from Dominica by Miller (1902:399). Later, Shamel (1928:67) named *Natalus dominicensis*, based on a series of funnel-eared bats from Dominica, the largest of which was selected as the holotype. Goodwin (1959) in his revision of the subgenus *Natalus*, demonstrated that Gray's holotype of *stramineus* (which is from an unknown locality) clearly resembled Lesser Antillean specimens, and restricted the type locality to Antigua. According to Goodwin (1959:5): "Examination of topotypes of *N. dominicensis* Shamel show that they agree in all essential characters and cranial measurements with the type of *N. stramineus* Gray." We agree with Goodwin that all Lesser Antillean specimens should be referred to a single subspecies. Howes' (1930:101, 103) report of two kinds of *Natalus* on Dominica, evidently based on presumed differences in size and color, is incorrect.

Table 2 presents the measurements of males and females of *N. stramineus* from Dominica. The sample was tested for secondary sexual variation. Males averaged significantly larger than females in breadth of braincase ($P \leq 0.01$) and mastoid breadth ($P \leq 0.05$). Males average larger, although not significantly, than

females in five of the other characters and average the same in only two (condylobasal length and postorbital constriction).

Using mainland data as reference points, we agree with Jones (1989) that *N. stramineus* probably reached the Lesser Antilles including Dominica from the north and west rather from the south as proposed by Koopman (1968, 1989). Based upon current data, Dominica is the southernmost geographic point of this northern invasion route into the Lesser Antilles.

As noted previously, the funnel-eared bat evidently is fairly common on Dominica, occurring wherever suitable retreats and foraging areas are available. The only roosts of record for the island are at Tanetane, where individuals were taken from a small cave in a sandy cliff along the beach of Douglas Bay (see account of *Pteronotus davyi*) and in a brick tunnel leading to some old ruins. This species has been reported from elsewhere as roosting in hollows of trees.

One of eight females netted at Trafalgar Falls on April 14, 1966, was lactating, but none of the others showed any indication of reproductive activity. In contrast, 20 of 25 females taken at Tanetane in early April of 1964 exhibited reproductive activity--19 were pregnant and one had a newly born young attached. Fetuses in four bats collected on April 4 measured 16.5, 20.0, 20.0, and 21.5; however, females collected from this same cave on July 27 evinced no reproductive activity. The testes of eight males taken on July 27 averaged 2.9 (2.5-3.5) in length.

Five non-pregnant (one lactating) April-taken females averaged 4.9 (4.6-5.3) in weight, whereas three males weighed 4.9, 5.0, and 5.2. Pregnant females collected in April weighed between 6.7 and 7.7.

Specimens examined in 1966 harbored the batfly, *Trichobius caecus* Edwards, a species known previously only from Trinidad.

Family VESPERTILIONIDAE

Eptesicus fuscus wetmorei Jackson
Big Brown Bat*Specimens examined*.—None.*Additional record*.—ST. PETER PARISH: Syndicate (Hill and Evans, 1985).

Remarks.—Our knowledge concerning the big brown bat on Dominica is based solely upon the report by Hill and Evans (1985). The basis of their report was four specimens of *Eptesicus fuscus* collected by Evans during ecological studies of the bat community on Dominica. The three females and one male were collected on September 8-9, 1982, September 9-10, 1983, and April 20, 1984, at Syndicate on the slopes of Morne Diablotin at 2000 ft [= 615 m]. The bats were taken under or at the edge of lower montane primary rain forest that was dominated by *Dacryodes excelsa* and *Sloanea* spp. The forest canopy was about 27 to 32 m high with a relatively dense understory of shrubs. Evans believed that *Eptesicus* was not uncommon in the primary rain forest and apparently roosted in trees such as *Sloanea*. Big brown bats were captured around dusk along with *Pteronotus*, *Natalus*, and *Myotis*, whereas later in the night the following bats were taken in the same area: *Ardops*, *Artibeus*, *Brachyphylla*, *Monophyllus*, and *Sturnira*.

The measurements of a male and female from Hill and Evans (1985:134) are presented in Table 6. The female is larger in five of the measurements reported in Table 6, the male is larger in three, and both measured 9.5 in mastoid breadth. These specimens are smaller, have shorted ears, and shorter tibia than the other known species of this genus in the Lesser Antilles, *Eptesicus guadeloupensis*, from the adjacent island of Guadeloupe (Genoways and Baker, 1975; Baker et al., 1978). Hill and Evans (1985) believed that the Dominican specimens most closely resembled *Eptesicus fuscus wetmorei* of Puerto Rico 700 kilometers to the northwest rather than populations in Central or South America. There is a much earlier record of *E. fuscus* from Barbados (Dobson, 1878), but most recent authors have considered this specimen to be an accidental occurrence or a mislabeled individual (Koopman, 1968; Genoways and Baker, 1975; Baker

Table 6.—Length of forearm and cranial measurements of representatives of two chiropteran families (*Vespertilionidae* and *Molossidae*) from Dominica.

Sex and statistics or catalog number	Length of forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Mastoid breadth	Breadth across upper molars	Length of maxillary toothrow
<i>Myotis dominicensis</i> (males)									
N	10	10	10	8	10	10	10	10	10
Mean	33.7	12.9	12.1	7.8	3.1	6.1	6.7	4.9	4.8
Minimum	33.0	12.7	11.9	7.6	3.0	6.0	6.6	4.8	4.6
Maximum	34.8	13.1	12.2	8.0	3.2	6.3	6.9	5.1	4.9
±SE	±0.22	±0.04	±0.04	±0.06	±0.03	±0.03	±0.03	±0.03	±0.03
<i>Myotis dominicensis</i> (females)									
N	10	10	10	9	10	10	10	10	10
Mean	34.0	12.8	12.1	7.9	3.1	6.1	6.7	5.0	4.8
Minimum	33.3	12.6	11.8	7.6	3.0	6.0	6.5	4.9	4.6
Maximum	34.6	13.1	12.4	8.1	3.2	6.3	6.9	5.2	4.9
±SE	±0.13	±0.07	±0.05	±0.05	±0.02	±0.04	±0.04	±0.03	±0.03

Table 6.—*cont.*

<i>Eptesicus fuscus wetmorei</i> ¹ (male)									
BNMH 84.1098	46.8	18.8	18.0	12.7	4.4	8.8	9.5	7.6	7.1
<i>Eptesicus fuscus wetmorei</i> ¹ (female)									
BNMH 84.502	46.2	19.4	18.5	13.0	4.3	8.6	9.5	7.8	7.4
<i>Tadarida brasiliensis antillarum</i> (males)									
N	10	10	10	10	10	10	10	10	10
Mean	36.9	15.7	14.5	9.3	3.6	7.5	8.8	6.6	5.6
Minimum	35.9	15.3	13.9	8.9	3.3	7.4	8.6	6.4	5.5
Maximum	38.0	16.1	14.8	9.5	3.6	7.6	9.0	6.7	5.8
±SE	±0.23	±0.07	±0.09	±0.06	±0.03	±0.02	±0.05	±0.03	±0.03
<i>Tadarida brasiliensis antillarum</i> (females)									
N	10	10	10	10	10	10	10	10	10
Mean	37.4	15.5	14.3	9.1	3.5	7.5	8.8	6.5	5.5
Minimum	36.0	15.1	14.0	8.8	3.4	7.4	8.2	6.2	5.3
Maximum	38.2	15.9	14.6	9.4	3.6	7.7	8.9	6.8	5.7
±SE	±0.25	±0.07	±0.06	±0.07	±0.03	±0.04	±0.07	±0.03	±0.05
<i>Molossus molossus molossus</i> (males)									
N	10	10	10	10	10	10	10	10	10
Mean	38.1	17.4	14.9	10.6	3.3	8.6	10.3	7.6	6.0
Minimum	36.5	16.8	14.4	10.2	3.2	8.2	9.7	7.4	5.9
Maximum	39.2	17.8	15.2	10.9	3.5	8.8	10.7	7.9	6.1
±SE	±0.25	±0.11	±0.07	±0.08	±0.03	±0.06	±0.09	±0.05	±0.03
<i>Molossus molossus molossus</i> (females)									
N	10	9	10	10	10	10	10	10	10
Mean	37.8	16.6	14.2	10.1	3.2	8.4	9.8	7.3	5.8
Minimum	36.0	16.4	13.9	9.8	3.1	8.2	9.6	7.0	5.6
Maximum	38.9	16.8	14.7	10.3	3.5	8.6	10.0	7.8	6.0
±SE	±0.26	±0.04	±0.08	±0.05	±0.04	±0.05	±0.04	±0.07	±0.04

¹Measurements from Hill and Evans (1985).

and Genoways, 1978; Baker et al., 1978). Hill and Evans (1985) believed that the specimen from Barbados may also agree with *E. f. wetmorei* and concluded that the distribution of *Eptesicus fuscus* in the Antilles needed further investigation.

***Myotis dominicensis* Miller**
Dominican Myotis

Specimens examined (102).—ST. JOHNS PARISH: Portsmouth, 18 (KU 104931-48). ST. JOSEPH PARISH: 0.5 mi. W Bells, 800 ft, 10 (KU 104949-58); Clarke Hall Estate, 48 (KU 104959-71, TTU 31487-17, NMNH 361911-13, 391249); 1 mi. above mouth Layou River, 5 m, 2 (TTU 31518-19). PARISH UNKNOWN: Dominica, 24 (MCZ 17840, NMNH 113535, 113544-50, 113553-58, 113560, 113562-69).

Additional record.—ST. PETER PARISH: Syn-dicate (Hill and Evans, 1985).

Remarks.—This small vespertilionid, presently known only from Dominica, is widely distributed and common on the island. Originally named (Miller, 1902:253) as a species, *dominicensis* was relegated to subspecific status under *Myotis nigricans* by Miller and Allen (1925:183). It was treated as such in the literature until LaVal (1973) described a closely related species, *M. martiniquensis*, which he recorded from Martinique and Barbados. *M. dominicensis* differs from this species principally in smaller size and smaller tibia-forearm ratio. According to LaVal (1973:17), "...*dominicensis* and *martiniquensis* are rather distinct from the population of *nigricans* found in Venezuela, south of the Antilles. They are somewhat less distinct when compared with the total range of variation in *nigricans*, a species which exhibits a substantial degree of geographic variation over its vast two-continent range." We have maintained LaVal's arrangement here, but agree with the conclusion of Pedersen et al. (1996) and Genoways et al. (1998) that systematic review of Antillean *Myotis* is currently needed.

Nine external and cranial measurements were examined for secondary sexual variation (Table 6). None of the measurements revealed any significant secondary sexual variation and, in fact, means for males and females were the same for five of the measure-

ments. Females averaged larger in three of the remaining measurements (length of forearm, zygomatic breadth, and breadth across upper molars) and males were on the average larger in greatest length of skull.

Howes (1930:101-102) reported that *Myotis* was taken in 1926 at a place called "Stinking Hole" ("high in the hills above our headquarters," which in 1926 was at Corona House). No specimens were found at Stinking Hole when Howes returned in 1930. In 1929, specimens were taken at "Glo Manioc Cave." "There were very few bats in the cave. We found one mass of them quite near the entrance, from which I caught fifty or sixty in my net." This was "the only colony in the cave." Howes (1930:102) commented that guano was taken from the cave during this time.

These small myotis were taken in a variety of netting situations at night and from roosts during the day. At Clarke Hall Estate in March and April 1966, these bats were taken along with *Artibeus jamaicensis* in nets set across a trail adjacent to a banana grove and open vegetable plots. On April 5, 1966, a single female was captured in an insect net as it flew about the rooms in Clarke Hall at 2000 hours. Jones on March 30, 1966, and Jones and Phillips on August 31, 1967, visited a cave about 1/2 mile west of Bells believed to be the cave referred to by Howes as "Glo Manioc Cave." The cave is located on a hillside about 60 m above a tributary of the Layou River. On the first visit 200 to 300 individuals were observed in a single, tightly-packed group on a back wall of the main cavern. Of the approximately 50 individuals examined all were males. The bats seemed partially torpid, although some flew when disturbed. On the second visit, only two *Myotis* and one *Artibeus* were observed. One of the *Myotis* was wedged in a narrow crevice and seemed lethargic when disturbed. Jones obtained 18 individuals at Portsmouth (Fig. 5) on April 1, 1966, in the bell tower of a Catholic Church. The bats were observed in two clusters each composed of about 100 individuals. The clusters were roosting about 2 m apart on the slanting wooden wall above the bell.

At least 30 Dominican myotis were captured on the evening of July 24, 1978, in two mist nets placed across a branch of the Layou River via a suspended walking bridge in a coconut grove near Clarke Hall. This was a small riparian stream with large cleared



Figure 5.—A view looking south from the Cabrits Peninsula towards Portsmouth, St. John Parish, Dominica.

and overgrazed cattle pastures along both sides of the creek. Well before dark, Baker and Jones observed a swarm of small bats flying across the pasture. There was considerable organization to the group and it almost appeared like flocking behavior. Clearly the group remained closely knit and organized in a ball shape. The group came across the pasture then moved down the creek on one side of the tree line. When they reached the nets several were caught, which called vocally resulting in others becoming entangled. The swarm then moved off and out of sight but retained its swarming organization. Baker estimated the size of the group, which contained both males and females, as several hundred individuals.

Seventeen of 24 females obtained in the first half of April were pregnant. The embryos described as early to mid-term with a crown-rump length varying from 7 to 12 with a mean of 9.2. Ten males taken on March 30, 1966, had testes that averaged 2.7 (2.0-3.0) in length. Of 15 females examined between July 20 to 25, 1978, three evinced no reproductive activity, whereas the remaining 12 were lactating. Six males taken during this same time period had a mean length of testes of 3.0 (2.0-4.0). Three of these males were molting on their venters. Our reproductive data for *M. dominicensis* appear to be consistent with the sea-

sonal polyestry found in mainland populations of *Myotis nigricans* (Wilson and Findley, 1970; Fleming et al., 1972; Wilson 1973a), although our data represent only part of the annual cycle.

Ectoparasites collected from individuals of *M. dominicensis* included batflies, *Trichobius pseudotruncatus* Jobling.

Family MOLOSSIDAE

Tadarida brasiliensis antillarum (Miller) Brazilian Free-tailed Bat

Specimens examined (305). —ST. ANDREW PARISH: Là Haut, 1 (NMNH 113187); Marigot, 100 ft, 1 (KU 104989). ST. DAVID PARISH: Fond Figs River, near Castle Bruce, ca. 50 ft, 10 (NMNH 361921, 391260-68); 2 mi. SW Castle Bruce, 800 ft, 2 (KU 104990-91). ST. GEORGE PARISH: Castle Comfort Estate, 1 mi. SE Roseau, 30 ft, 36 (KU 105005-40); 0.5 mi. S Loubiere, 11 (KU 152140-50); Morne de Moulier, 20 (NMNH 303210-29). ST. JOHN PARISH: Cabrit, 9 (NMNH 391253-59, 361917-18); 1 mi. NW Portsmouth, 8 (KU 104972-79); Portsmouth, 20

ft, 9 (KU 104980-88). ST. JOSEPH PARISH: Clarke Hall Estate, 100 ft, 26 (KU 104992-98, 110256-62, NMNH 361914-15, 361919-20, 362111-13, 391250-52, 391273-74); Stone Estate, 15 (NMNH 113642-51, 113654, 113661-64). ST. LUKE PARISH: South Chiltern Estate, 3 (NMNH 361922, 362109-10). ST. PATRICK PARISH: Belvedere Estate, 8 (NMNH 113652-53, 113655-60); Geneva Estate, 9 (NMNH 113661-32, 113634-40); La Plaine, 200 ft, 2 (KU 105004, NMNH 361916). ST. PAUL PARISH: Antrim Valley, 17 (TTU 31563-79); 2.5 mi. S Layou [*in* St. Joseph Parish], 6 (KU 152134-39); Rodney's Rock, 96 (NMNH 361955-362045, 362105-08, 361923); 6 mi. NE Roseau, 2 (KU 152151-52); Springfield, 4 (TTU 31580-83); Sylvania Estate, 1800 ft, 5 (KU 104999-105003); Tarou Point, 1 (NMNH 391287). PARISH UNKNOWN: Dominica, 4 (MCZ 17843, 17883, NMNH 241115-16).

Additional records.—ST. GEORGE PARISH: Roseau (Miller, 1902). PARISH UNKNOWN: Dominica (Shamel, 1931).

Remarks.—Several closely related subspecies of this free-tailed bat occur in the Antillean region. *Tadarida brasiliensis antillularum* is the race distributed from Puerto Rico southward to St. Vincent (Vaughan and Hill, 1996). The subspecies was described by Miller (1902:398) with a type locality of Roseau, Dominica. The species presently is unknown from Barbados, the Grenadines, Grenada, Trinidad, excepting for one possibly accidental record from Tobago, and adjacent northern South America. *T. brasiliensis* is one of the most conspicuous and abundant bats on many Antillean islands.

Originally described as a species (Miller, 1902; Shamel, 1931), *antillularum* currently is regarded as a subspecies of the wide-ranging *T. brasiliensis*. However, *antillularum* and related Antillean races are small, brownish, sedentary bats in contrast with the larger, usually grayish, migratory populations of much of the mainland range of *brasiliensis*. Jones and Phillips (1970:142) wrote as follows: "owing to (1) the apparent absence of bats of the species *brasiliensis* from Trinidad and the north coast of South America, and apparently also the southern Lesser Antilles, and (2) the morphological and behavioral features that set Antillean populations apart from at least some on the North and Middle American mainland, the specific sta-

tus of *Tadarida* in the Antilles is in need of critical re-evaluation. Two alternative possibilities are: (1) *antillularum* and other Antillean populations represent a distinct species, or (2) they are related specifically to some population on the North American mainland, possibly *cynocephala*, of the southeastern United States, but not to others." *Tadarida b. cynocephala* is currently treated as a subspecies of *brasiliensis* (Schwartz, 1955; Barbour and Davis, 1969; Spenrath and LaVal, 1974; Schmidly et al., 1977; Owen et al., 1990; Schmidly, 1991), but Owen et al. (1990) have provided evidence that the non-migratory Antillean populations may have arisen from non-migratory populations in the southeastern U.S. rather than the migratory populations *T. brasiliensis* in the southwestern U.S., Mexico, and Central America. We have maintained *antillularum* as a subspecies of *brasiliensis*, with the idea that systematics of the entire complex of these free-tailed bats needs to be reviewed before individual taxonomic changes should be made as was done by Owen et al. (1990) for *T. b. cynocephala*.

Males were significantly ($P \leq 0.05$) larger than females in the only three cranial length measurements (greatest length of skull, condylobasal length, length of maxillary toothrow) presented in Table 6. The means for the sexes were not significantly different for the length of forearm and the five cranial breadth measurements (Table 6). Of these six measurements, males averaged larger in three (zygomatic breadth, postorbital constriction, and breadth across upper molars), females average larger in length of forearm, and both sexes average 7.5 in breadth of braincase and 8.8 in mastoid breadth.

Brazilian free-tailed bats have been taken in four general situations on Dominica.—1) in caves or similar shelters, 2) associated with human constructed features, 3) netted over bodies of open water, or 4) shot in large openings in vegetation. Specimens were taken in coastal caves at Rodney's Rock and at the same or nearby cave near the point at Tarou Point. There was a colony of *Tadarida* in a cave 1 1/2 miles northwest of Mahaut, although no specimens were preserved. The cave was about 9 m deep and 12 m wide with the bats roosting in cracks between larger rocks in the ceiling. At 2 miles southwest of Castle Bruce, specimens were taken from the interconnected vertical cracks in a cliff wall (Fig. 6). Free-tailed bats also were taken from the ruins and the tunnels at the old



Figure 6.—East coast of Dominica near Castle Bruce, St. David Parish.

fort near Cabrit. At Castle Comfort Estate a sample of 36 individuals were taken from a colony of several thousand in a storeroom. The majority of the colony was located between a wall and a beam that was a few centimeters from the wall. The overflow of several hundred from the colony was clustered on the wall below the beam about 10 m above the floor. At Clarke Hall Estate, individuals were taken on several occasions from behind shutters and shingles of the main building and some were caught inside of the house. Eight *Tadarida* and *Molossus* also were taken from behind a shutter at Springfield. Nine free-tailed bats were taken from a colony in the attic of the Catholic Church in Portsmouth. Individuals of *Tadarida brasiliensis* were taken from between the boards and corrugated tin roofs of buildings at Sylvania and Morne de Moulrier. Sylvania, at more than 550 m in elevation, is the highest locality from which we have recorded this species; the population was estimated at several hundred bats. Brazilian free-tailed bats were netted over a pool in the Fond Figues River near Castle Bruce, over the water works tank in Antrim Valley, in the open areas and over the Layout at Clarke Hall Estate, and under large mango trees at Springfield. Free-tailed bats were shot as they flew over open areas at Clarke Hall Estate and a single female was shot near Marigot as it flew over the beach at dusk.

Females taken on the following dates evinced no reproductive activity: March 20(1); March 24 (1); April 1 (4); April 11 (3); April 16 (1). In contrast, four females taken at Springfield on July 19 evinced lactation (1), no gross reproductive activity (1), and two carried single fetuses that measured 22. Fourteen females were captured at Antrim Valley on July 21 of which 10 were lactating, two carried single embryos measuring 23, 24, and two revealed no gross reproductive activity. Five of six females captured at Clarke Hall Estate on September 1 were lactating. Five males taken on March 24 had testes measuring 5.7 (5-6) in length, four from April 7 to 17 were 5.25 (4.5-6.0), and three males taken on July 21 all had testes measuring 4. The average weight of 23 males was 8.6 (6.3-10.3), whereas 14 females averaged 9.1 (7.5-12).

Molossus molossus molossus (Pallas)
Pallas' Mastiff Bat

Specimens examined (165).—ST. DAVID PARISH: Castle Bruce, 6 (NMNH 361925-26, 391269-72). ST. GEORGE PARISH: Roseau, 12 (NMNH 113226-37). ST. JOHN PARISH: Portsmouth, 20 ft, 1 (KU 105041). ST. JOSEPH PARISH: California Estate, 1 (KU 152113); Clarke Hall Estate, 100 ft, 13

(KU 105043-52, NMNH 361924, 391288-89). ST. PAUL PARISH: Antrim Valley, 20 (TTU 31520-39); 2.5 mi. S Layou [*in* St. Joseph Parish], 7 (KU 105106-12); Mt. Joy Estate, 10 (TTU 63375-84); Pont Cassé, 1850 ft, 1 (KU 105042); Rodney's Rock, 55 (NMNH 362046-94, 362114-17, 361927-28); Springfield, 3 (TCWC 55726-27, TTU 31540). PARISH UNKNOWN: Dominica, 38 (MCZ 6025-7, NMNH 113191-225).

Remarks.—"This common house bat probably occurs on virtually every Lesser Antillean island," according to Koopman (1968:9) and is widely distributed elsewhere in the Antilles as well. Historically, several specific names have been applied to Antillean populations, but these are now all best regarded as pertaining to *Molossus molossus*, a small mastiff bat with pale-based hairs that is distributed widely in the Neotropics. The subspecies *M. m. molossus* is thought to occur in the Lesser Antilles (Dolan, 1989), with the type locality being Martinique (restricted by Husson, 1962). Dolan (1989) assigned material from northern South America to *M. m. minor* Kerr and specimens of this species from the Great Antilles to *M. m. tropidorhynchus* Gray. The nominate subspecies appeared to Dolan to be more closely related to *minor* of northern South America than *tropidorhynchus* of the Great Antilles; therefore she proposed a dual invasion of *M. molossus* into the Antilles, with *M. m. molossus* entering from the south.

G. M. Allen (2908:59-60; 1911:249-250) erroneously assigned Dominican specimens of different sexes to two different species of *Molossus* because he failed to appreciate the significant secondary sexual dimorphism present in these bats. In our sample from the island, males averaged significantly larger than females in all eight cranial measurements examined (Table 6) and males averaged larger than females in length of forearm, but the difference was not significant. The differences in cranial measurements were significant at the $P=0.001$ level for five characters (greatest length of skull, condylobasal length, zygomatic breadth, mastoid breadth, and length of maxillary toothrow), at the $P=0.01$ level for breadth across the upper molars, and at $P=0.05$ for postorbital constriction and breadth of braincase. The secondary sexual differences in this

species are far more important than in the other member of the family, *Tadarida brasiliensis*, occurring on the island.

Pallas' mastiff bats were taken along with the Brazilian free-tailed bats at many of the same places and under the same circumstances. In fact, we have records of *M. molossus* at only four localities where they were not taken with *T. brasiliensis*—Pont Cassé, California Estate, Roseau, and Mt. Joy Estate. For the environmental conditions where these two species were captured together see the previous account. At Pont Cassé, the specimen and another individual that escaped were found between the board and corrugated steel of the roof of a forestry station. At 570 m, this is the highest elevation that this mastiff bat was captured on Dominica. In Roseau, specimens were taken in a house. Pallas' mastiff bats were caught in nets placed in open areas around the buildings and adjacent to the surrounding vegetation at Mt. Joy Estate.

Females taken on March 20 and 24 were not pregnant as were seven of 10 females taken on April 1; however, the three other females taken on April 1 evinced the earliest stages of pregnancy. Pregnant females (crown-rump length of single embryos in parentheses) were taken on April 10 (6), April 11 (12), April 19 (9), June 1 (23), and July 8 (25). Females taken on July 9 and 10 revealed evidence of lactation as did 11 of 12 females taken on July 21. The remaining female from July 21 evinced no gross reproductive activity. Six males taken between April 1 and 9 have testes that averaged 5.7 (5-6) in length and one taken on June 1 had testes measuring 5.5, whereas six males taken July 21 have testes that only averaged 4 (2-6) in length. A hairless non-flying young female was taken along with its mother on October 5, 1899. The forearm of this young animal was 21.6. Subadult flying individuals still evincing unfused phalangeal epiphyses were taken on August 5, 1901 (one female and two males), and October 5, 1899 (one male). The length of forearms of these individuals, respectively, were 37.5, 37.6, 37.8, and 38.0. Comparing these measurements with those for adults in Table 6 indicates that these subadults had reached adult size. The weight of 9 males averaged 14.7 (13.4-16.7), whereas 14 females only averaged 12.6 (10.0-15.3) in weight.

DISCUSSION

As understood herein, the chiropteran fauna of the island of Dominica is composed of 12 species. These 12 species represent six families, including Mormoopidae (1 species), Noctilionidae (1), Phyllostomidae (5), Natalidae (1), Vespertilionidae (2), and Molossidae (2). Within the family Phyllostomidae, two Tribes—Glossophagini (2) and Sternodermatini (3)—of the subfamily Phyllostominae are represented (Baker et al., 1989:234). A thirteenth species of bat—*Glossophaga longirostris*—has long been considered to be a member of the chiropteran fauna of Dominica. Miller (1913a, 1913b) was the first to report the species from the island. However, Handley and Webster (1987) have conclusively shown that this record is based upon mislabeled and mismatched specimens that were actually from Grenada.

Areography

The chiropteran fauna of Dominica contains one species—*Myotis dominicensis*—and two subspecies—*Ardops nichollsi nichollsi* and *Sturnira lilium angeli*—endemic to the island. This is a typical level of endemism for most islands in the Lesser Antilles, but below the level of Guadeloupe where “most of the evolutionary activity of the Lesser Antillean bat faunas has been associated” (Baker and Genoways, 1978; Baker et al., 1978). The geographic range of the species *Ardops nichollsi* is confined to the Lesser Antilles from St. Eustatius in the north to St. Vincent in the south. *Brachyphylla cavernarum* is found from St. Vincent and Barbados in the south northward through the remainder of the Lesser Antilles and in the Virgin Islands and Puerto Rico in the Greater Antilles. The geographic range of *Monophyllus plethodon* follows the pattern as that of *B. cavernarum*, although the population in the Greater Antilles is only represented by a fossil known from Puerto Rico. All three of these genera—*Ardops*, *Brachyphylla*, and *Monophyllus*—are endemic to the Antillean islands.

The geographic distribution of *Noctilio leporinus* and even the subspecies *mastivus* give no real clue as to how it has reached the island of Dominica. This bat is a powerful flyer and is accustomed to flying over water. The species is widespread around the Caribbean and Gulf of Mexico, possibly limited only by the

availability of roost sites. The remaining members of the chiropteran fauna of Dominica have reached the island by invasion either from the South American mainland to the south or from the Greater Antilles or the Mexico and Central American mainland from the north and west.

Based upon our own studies and those of other investigators, there are apparently three species—*Pteronotus davyi*, *Sturnira lilium*, and *Molossus molossus*—that have arrived on Dominica from the south. The distribution of *P. davyi* in the Lesser Antilles is disjunct, but its furthest north known population is on Marie Galante (30 km) just to the northeast of Dominica. The species is known in South and Central America, but is absent in the northern Lesser Antilles and the Greater Antilles, where several other members of the genus are known to occur. The population of *Sturnira lilium* is the northernmost of a series occupying Martinique, St. Lucia, St. Vincent, Grenada, Tobago, Trinidad, and finally the South American mainland (Jones and Phillips, 1976; Genoways et al., 1998). The only *Sturnira* to the north of Dominica is the closely related, but distinct, Antillean endemic *Sturnira thomasi* from Guadeloupe and Montserrat. The exact relationships of the *Molossus molossus* populations is more problematic, but Dolan (1989:63–65) studying this species concluded that *M. m. molossus* was more closely related to *M. m. minor* in northern South America rather than *M. m. debilis* and *M. m. fortis* of the northern Lesser Antilles and the Greater Antilles, which Dolan concluded were related to populations in Mexico and Central America.

Reaching Dominica from the north and west are four species of bats—*Artibeus jamaicensis*, *Natalus stramineus*, *Eptesicus fuscus*, and *Tadarida brasiliensis*. Considerable work has been undertaken in recent years on the relationships of Antillean populations of *Artibeus jamaicensis* by Phillips et al. (1989, 1991) and Pumo et al. (1988, 1996). They determined that populations as far south in the Lesser Antilles as St. Lucia and Barbados have their relationship to the north in the Greater Antilles and Yucatán Peninsula. The population on St. Vincent is unique and may represent an older, far more widespread gene pool. To the south, Grenada populations are morphologically distinct, but

are genetically more closely related to populations on Trinidad. The distribution of *Tadarida brasiliensis* is much the same with the southernmost known population recently being reported from St. Vincent (Vaughan and Hill, 1996), with the possible exception of a single specimen known from Tobago (Eschelman and Morgan, 1985).

Until recently, the distribution of *Natalus stramineus* in the Lesser Antilles has been difficult to explain; however, Varona (1974) considered *Natalus major* of the Greater Antilles conspecific with *stramineus* and served to connect to the mainland populations of the species in Mexico and Central America. The population of *stramineus* on Dominica is the southernmost in the Lesser Antilles and *Natalus tumidirostris* occupies Trinidad and Tobago so a connection to the south for *N. stramineus* seems implausible. The most enigmatic species distribution on Dominica currently is *Eptesicus fuscus* (Hill and Evans, 1985). The species approaches Dominica from the north no closer than to Puerto Rico to which subspecies the Dominican specimens are currently assigned. There is an old record from Barbados that has generally been discounted until the discovery of the Dominican population (Hill and Evans, 1985; Koopman, 1989). The problem is confounded by the fact that *Eptesicus guadeloupensis* is known from Guadeloupe, the island

just to the north of Dominica (Genoways and Baker, 1975; Baker et al., 1978). *E. guadeloupensis* is a member of the *fuscus* group in the genus, but its distinctive characteristics mark it certainly as a separate species.

It can, therefore, be concluded that the fauna of Dominica is composed of a minor endemic element and major invading elements from both the north and south. Given its central position in the Lesser Antilles, this result should not be overly surprising. This central position with invasions as regular events certainly has kept the level of endemism among bats on the island at a low. However, under similar circumstances Guadeloupe (approximately 40 km north of Dominica) has a fauna considerably richer in endemics, including three endemic species and one endemic subspecies.

Examining the areographic relationships of the species occurring on Dominica revealed that three faunal elements are represented on the island. The Neotropical Chiropteran Fauna represents 50% of the species on the island, including *Pteronotus davyi*, *Noctilio leporinus*, *Artibeus jamaicensis*, *Sturnira lilium*, *Natalus stramineus*, and *Molossus molossus*. All of these species have broad distributional patterns in the Neotropical areas of Mexico, Central America, and South America. The Antillean Chiropteran Fauna is represented by *Ardops nicholli*, *Brachyphylla*

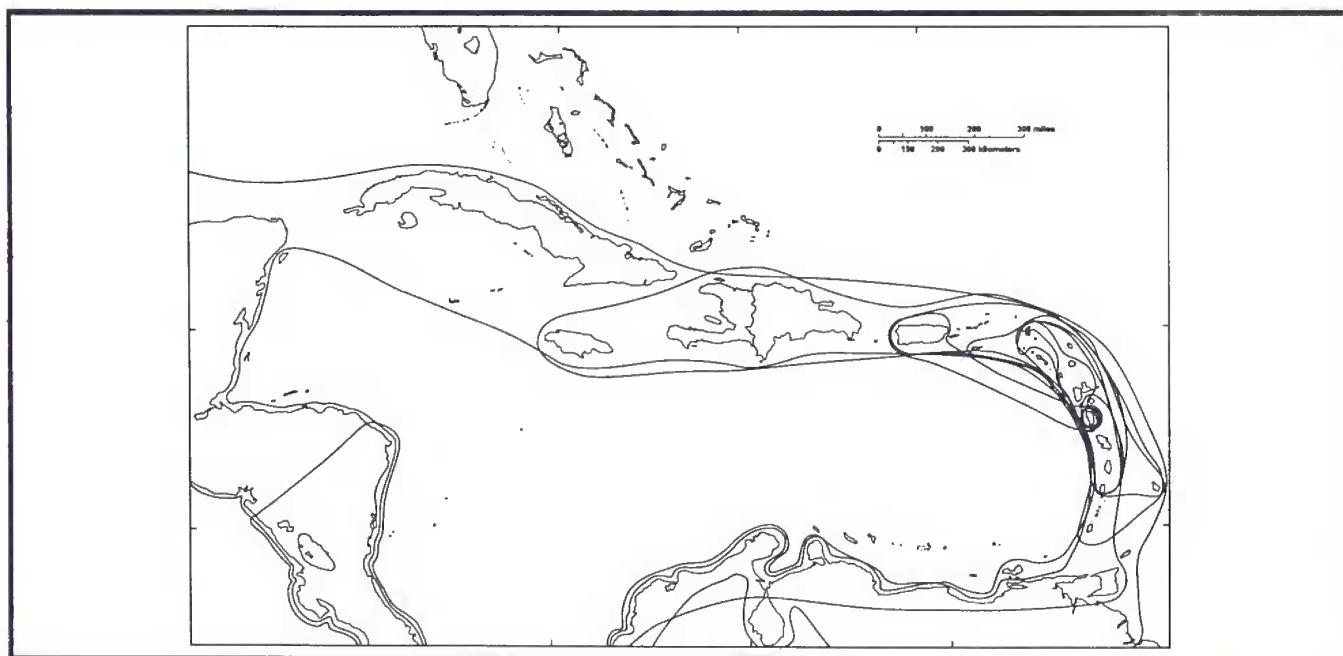


Figure 7.—An areographic map for the chiropteran fauna of Dominica.

cavernarum, *Monophyllus plethodon*, and *Myotis dominicensis*. It is somewhat surprising to find an island in the Antillean chain that does not have 50% or more of the fauna represented by species of the Antillean Chiropteran Fauna. Only *M. dominicensis* is endemic to Dominica and *A. nichollsi* is confined to the Lesser Antilles. The other two species occur primarily in the Lesser Antilles, but do reach the Greater Antilles as far as Puerto Rico (*M. plethodon* as a fossil). The remaining two species—*Eptesicus fuscus* and *Tadarida brasiliensis*—represent a Nearctic/Neotropical Chiropteran Fauna. These species have extensive distributions in the United States and southward into the Neotropical Faunal Zone.

An areographic map (Fig. 7) based upon the distributional patterns of the monotypic species and subspecies occurring on Dominica is quite instructive. Dominica appears to fall into a group of Lesser Antillean islands consisting of Montserrat and Guadeloupe to the north and Martinique, St. Lucia, and St. Vincent to the south. We propose considering this region to be the Lesser Antillean Faunal Core. However, more complete faunal surveys of the three islands to the south of Dominica will need to be completed before a thorough analysis of this faunal core region can be completed. Antigua may also belong with this group, but more data also are needed on the chiropteran fauna of this island before a final decision can be made.

The difficulties we encounter in deciphering distributional patterns for bat species, and in determining the position of Dominica within Antillean biogeography, call attention to the subtle role of historical factors. It is always tempting to think that documentation of species occurrence through collecting provides a "final" picture of bat distributions and that this picture in turn is the end product of dispersal and local evolution. In fact, however, this data set (as it currently stands) is full of conflicts and contradictions. One of the most obvious is the difference between the bat faunas of Dominica and Guadeloupe. It might be realistic to think that some aspects of distribution are simply stochastic. Moreover, it is essential to remember that occurrences—indeed, faunal composition on any island—are not necessarily permanent. Thus, numbers of endemics at this moment in time does not necessarily reflect any former time, especially if one recalls that bat species of one sort or another have probably been in the Antilles at least since the Pliocene.

Genetic data (Pumo et al., 1996; Genoways et al., 1998; Phillips et al., unpublished) and fossil evidence from Cuba (Silva Taboada, 1979) clearly show that there have been at least three separate invasions of the Jamaican fruit bat, *Artibeus jamaicensis* (or closely-related species). The earliest invasion must have been in the Pliocene (~2 million years before present), whereas the most recent one was in the Late Pleistocene or Holocene (~12,000 years ago) (Phillips et al., 1989; Pumo et al., 1996). There are two relevant lessons in this data set. First, although the Jamaican fruit bat is a common, geographically widespread Neotropical bat species, significant genetic structuring occurs among islands. Second, this genetic structuring and complex dispersal history are not readily apparent just from records of distribution or examination of morphology. Thus, we suspect that our areographic analyses might look somewhat different if we had access to (1) genetic data for all the species, and (2) some means of sorting or identifying patterns within a historical context.

Trophic Structure

The trophic structure of the chiropteran fauna of 22 Caribbean islands and banks, and, for comparison, four mainland areas of Mexico, Nicaragua, Venezuela, and Suriname is present in Table 7. We have used the feeding guild classification system presented by Wilson (1973b) rather than the more complex systems used by other recent authors (Findley, 1993; Willig and Mares, 1989; Willig and Gannon, 1996) because it seems to be a better fit for the chiropteran fauna of the Caribbean islands. We have not arranged these data into morphological matrices as was done by some other authors (Fleming et al., 1972; Smith and Genoways, 1974) because Willig (1986) has shown "These matrices obscure more information than they reveal concerning...bat community organization" and Willig and Moulton (1989) and Willig et al. (1993) concluded that in Neotropical bat communities "ecomorphological structure [was] indistinguishable from that produced by stochastic processes." Rodríguez-Durán et al. (1993) studying insectivorous bats on Puerto Rico found that "morphological trends reveal only part of the answer to the question of what influences the diet of bats;" however, it should be noted that Fleming (1991) did find that in the genus *Carollia* patterns of diet were associated with body size. Finally, so many

Table 7.—Trophic structure of the chiropteran fauna of 22 Caribbean islands and banks and 4 mainland areas.

Island or Bank (No. of species in fauna) ¹	Carn	Pisc	Sang	Fol Gle	Aer Ins	Frug	Nect
Nicaragua (85)	3.8	1.2	3.4	11.8	40.5	31.1	8.2
Yucatan Peninsula (48)	4.2	2.1	4.0	14.6	48.9	23.9	2.3
Jamaica (21)	0	4.8	0	5.7	63.8	9.0	16.7
Cuba (26)	0	3.8	0	5.8	67.7	10.0	12.7
Hispaniola (18)	0	5.6	0	3.9	57.8	14.4	18.3
Puerto Rican bank (13)	0	7.7	0	3.1	53.1	17.7	18.4
St. Croix (4)	0	25.0	0	5.0	25.0	27.5	17.5
St. Martin bank (8)	0	12.5	0	5.0	48.8	15.0	18.7
St. Kitts bank (6)	0	16.7	0	3.3	33.3	35.0	11.7
Antigua bank (7)	0	14.3	0	4.3	42.9	17.1	21.4
Montserrat (11)	0	9.1	0	2.7	36.4	38.2	13.6
Guadeloupe (11)	0	9.1	0	2.7	36.4	38.2	13.6
Dominica (12)	0	8.3	0	2.5	50.0	26.7	12.5
Martinique (10)	0	10.0	0	4.0	39.0	32.0	15.0
St. Lucia (8)	0	12.5	0	3.7	25.0	40.0	18.8
St. Vincent (12)	0	8.3	0	8.3	25.0	38.4	20.0
Barbados (7)	0	14.3	0	5.7	41.5	17.1	21.4
Grenada (12)	0	8.3	0	7.5	33.3	33.3	17.5
Tobago (20)	1.0	5.0	0	7.5	39.0	41.0	6.5
Trinidad (64)	3.8	1.6	3.0	14.0	41.4	29.8	6.4
Suriname (95)	3.6	0.6	2.1	15.3	40.3	29.1	9.0
coastal Venezuela (39)	3.8	1.5	7.4	12.6	40.8	26.9	6.9
Margarita (16)	0	3.8	11.9	7.5	43.1	22.5	10.6
Bonaire (7)	0	0	0	1.4	57.1	18.6	22.9
Curaçao (8)	0	7.5	0	2.5	55.0	15.0	20.0
Aruba (4)	0	0	0	2.5	50.0	7.5	40.0

¹Species present in bat faunas based upon reports in Baker et al. (1978), Birney et al. (1974), Carter et al. (1981), Eshelman and Morgan (1985), Genoways et al. (1981, 1998), Genoways and Williams (1979a, 1979b, 1980, 1986), Husson (1960, 1978), Jones (1989), Jones and Baker (1979), Jones et al. (1971, 1973), Jones and Owen (1986), Kock and Stephan (1986), Koopman (1989), Morgan and Woods (1986), Pederson et al. (1996), Sanchez-Herrera et al. (1986), Smith and Genoways (1974), Vaughan and Hill (1996), Webster and Jones (1980), Williams and Genoways (1980a, 1980b), Williams et al. (1983).

open cells remain in the matrices with the small chiropteran faunas of the Caribbean islands that these missing data obscure the actual patterns (Smith and Genoways, 1974).

The feeding guilds in their order of importance on Dominica were as follows: aerial insectivore guild, 50%; frugivore, 26.7%; nectivore, 12.5%; piscivore, 8.3%; foliage gleaning, 2.5% (Table 7). The carnivore and sanguinivore feeding guilds are not represented in the chiropteran fauna of Dominica nor in the faunas of any of the other West Indian islands. As Rodríguez-Durán and Kunz (2000) correctly noted, the lack of any large mammals or birds in the modern faunas of these islands could account for the absence of the sanguinivores, which were on Cuba when ground sloths were present. However, the absence of carnivorous species taking frogs, lizards, and small birds is not easily explained. This guild was only represented on the islands of Trinidad and Tobago, among the islands that we have reviewed here. Likewise, sanguinivory is represented only on Trinidad and Margarita. These three islands (Trinidad, Tobago, and Margarita) are the largest of the coastal South American islands included here and the presence of these two guilds is probably best explained by the proximity of the islands to the potential source area of South America, and the presence of suitable food, including livestock.

As concluded by Rodríguez-Durán and Kunz (2000) to be true for West Indian islands, the fauna of Dominica is dominated by aerial insectivores and frugivores. It should be noted, however, that Dominica is the only island in the Lesser Antilles where the aerial insectivore guild accounts for at least 50% of the fauna. This high percentage of aerial insectivores also is true for the chiropteran faunas of the Greater Antillean islands of Jamaica, Cuba, Hispaniola, and Puerto Rican bank and the small, dry South American coastal islands of Bonaire, Curaçao, and Aruba. For the majority of the islands and mainland sites studied by us, the aerial insectivore guild represents a higher percentage of the chiropteran fauna than the frugivore guild. The exceptions to this observation are five islands or banks in the Lesser Antilles—St. Kitts bank, Montserrat, Guadeloupe, St. Lucia, and St. Vincent—St. Croix, and Tobago. These islands in the Lesser Antilles in-

clude those immediately to the north and also the south of Dominica.

The nectivorous guild is more highly represented in the West Indian bat faunas than any of the mainland and other island (Trinidad, Tobago, and Margarita) faunas except for the small dry coastal islands of Bonaire, Curaçao, and Aruba. The opposite pattern is exhibited by the foliage gleaning guild in which the higher percentages are represented in the chiropteran faunas of Trinidad and the mainland sites, whereas lower percentages are found in the faunas of the islands of the West Indies and Bonaire, Curaçao, and Aruba. The only exceptions to this reversal of guild percentages are the faunas of Tobago and Margarita. The foliage gleaning guild is represented on these two island at percentages that are as low as some found for the West Indian faunas (7.5% for both faunas).

The piscivorous guild is represented solely by members of the genus *Noctilio* and most cases solely by *Noctilio leporinus*. The significance of this guild varies greatly from island to island depending upon the size of the chiropteran fauna of the island. The presence of this one species is far more significant on an island with only four species of bats, for example St. Croix, than in a place such as Suriname where there are at least 95 species of bats.

The pattern of trophic guilds represented on Dominica generally conform to those represented by other West Indian bat faunas, rather than those of mainland sites or large coastal South American islands. However, some of the details of the guild structure of the fauna from Dominica more nearly resembles that of the islands of the Greater Antilles than other islands in the Lesser Antilles. This may be because Dominica remains the most pristine of any in the Lesser Antilles. Consequently, its chiropteran fauna might more closely resemble those of the larger islands, with more diverse habitats. If this is the reason for the present trophic guild structure of Dominica, we must wonder if the chiropteran faunas of the other Lesser Antillean islands have been changed through human actions of clearing original forests and introduction of non-native plants (including eucalyptus), and tropical agricultural practices.

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